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NITROGEN FIXATION IN A HIGH ARCTIC ECOSYSTEM

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Nitrogen Fixation in a High Arctic Ecosystem" submitted by R. Craig Stutz in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

Biological nitrogen-fixation was studied on Truelove Lowland, Devon Island, N.W.T., in three different habitats. Raised beach ridges, resulting from post-glacial uplift, form well-defined xeric habitats which are dominated by dwarf shrubs and cushion plants. Hummocky meadows dominated by sedges, mosses and forbs compose the second intensively studied habitat. Water-logged meadows of moss and sedge were studied less intensively.

Nitrogen-fixation was estimated using acetylene-reduction assay (Stewart, *et al.*, 1967). Incubation temperatures were moderated by immersing the incubation jars in water or burying them in a soil pit (10 cm) on site.

Soil algae populations were estimated by correlating field microscopic observations with dilution culture.

Available nitrogen was determined by micro-kjeldahl analysis of KCl soil-extracts.

Symbiotic nitrogen-fixation by vascular plants is nil on Truelove Lowland. One lichen species, *Peltigera aphthosa*, reduced acetylene (5.1 uumoles$\cdot$mg$^{-1}\cdot$hr^{-1}). *Nostoc commune*, a prominent blue-green algae on meadow soils, reduced acetylene at a rate 10 times that of *P. aphthosa*.

Soil algae populations were measured as high as 9.3×10^4 cells$\cdot$g soil^{-1} on beach ridges and 5.0×10^5 cells$\cdot$g soil^{-1} on meadows. *Nostoc* sp. usually accounted for 50 to 90% of the algal flora. Based on population data, acetylene-reduction data and hourly soil surface temperature data (Courtin, 1972), soil algae were estimated to fix 14 ug N$\cdot$m$^{-2}\cdot$yr^{-1} in meadows.

Nitrogen-fixation was greatest at the anaerobic-aerobic interface in soils, and was a function of anaerobic bacteria. Nitrate nitrogen applied to the soil at a rate of 1 ppm decreased fixation 56%. Normally nitrate is absent from these soils. The rate of fixation responded exponentially to temperature with an apparent Q_{10} of 5.6. An estimated 30 and 7 mg $N \cdot m^{-2} \cdot yr^{-1}$ was fixed on the beach ridges in 1971 and 1972 respectively, and 190 and 65 mg $N \cdot m^{-2} \cdot yr^{-1}$ was fixed on the meadows in the same years.

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The author is indebted to Dr. L. C. Bliss who supervised the preparation of this thesis at all stages. There are many who also contributed to the work at various phases. In particular, I recognize all those who worked on Devon Island with the IBP project. Mr. John Poirier, my field assistant, did his work well. Ms. Jan Marsh spent many hours with a microscope when she would often have preferred skis. Dr. G. M. Courtin contributed time, equipment, and concern much in excess of what was expected. Mr. P. A. Addison presented challenging conversation both in theoretical and practical aspects of the thesis. Drs. J. M. Mayo, P. Widden, D. L. Pattie, and D. G. Despain, and Messrs. T. A. Babb, J. Svoboda, M. Muc, P. Pakarinen, T. W. Peters, B. Walker, J. Ryan, and E. van Zinderen Bakker all contributed to this work through discussion which provided invaluable insight into the functioning of the Lowland ecosystem.

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Nevertheless, the author assumes full responsibility for data, interpretation of data and conclusions in this thesis.

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Permeating this acknowledgment is the support and faith of my wife, Priscilla, who was somehow able to motivate her husband, raise her children, and maintain her sanity throughout the entire project.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The efforts of International Biological Programme projects studying productivity have been focused on two chemical reduction processes, namely photosynthesis and nitrogen-fixation. Carbon is largely transitory, even structural carbon eventually being utilized as an energy substrate in the trophic system and returned to the atmosphere as carbon dioxide. Nitrogen is much more persistent in the biosphere. Only under unique conditions is it returned to the atmosphere. The rate of carbon fixation may be expressed in terms of kilograms$\cdot m^{-2} \cdot yr^{-1}$ (Whittaker, 1970) while nitrogen-fixation in terms of milligrams. (Costa Verdade, 1967).

Arctic tundra plants have been reported to be nitrogen deficient by several observers, but opinion as to cause has differed from actual low nitrogen concentration in the soil (e.g. Russell, 1940) to cryic inhibition of its uptake and utilization (Dadykin, 1958). Nitrogen fertilizers affect some arctic plants (Warren-Wilson, 1957; Haag, 1972), but not others (Babb, 1972). Whether the rate of nitrogen-fixation in high arctic tundras restricts productivity of these ecosystems has heretofore been a mute question.

Studies of nitrogen-fixation in natural systems were made feasible by the development of acetylene-reduction assays (Stewart et al., 1967). This assay, based on the observation that acetylene is a competitive inhibitor of nitrogen on nitrogenase (Dilworth, 1966), is sensitive, versatile and rapid, as is evidenced by its reported use in over 200 publications (Hardy et al., 1973). The assay involves incubating biological material in the presence of acetylene and measuring the rate of ethylene evolution. Ethylene can be detected in minute quantities

by gas chromatography or colorimetrically if it is in sufficiently high concentration (LaRue and Kurz, 1973). Ethylene production can be related to nitrogen-fixation by comparing acetylene-reduction with N^{15} assays or changes in total nitrogen content. Generally the ratio between acetylene-reduction and nitrogen-fixation is between 1.5:1 and 25:1 (Hardy *et al.*, 1973). For soil systems the C_2H_2:N_2 ratio is generally between 3 and 6.

This research was done in connection with the Canadian I.B.P. Project on the Truelove Lowland, Devon Island (Fig. 1). The objectives were to estimate the rate of biological nitrogen-fixation in different habitats, and to determine environmental and biological factors affecting this rate.

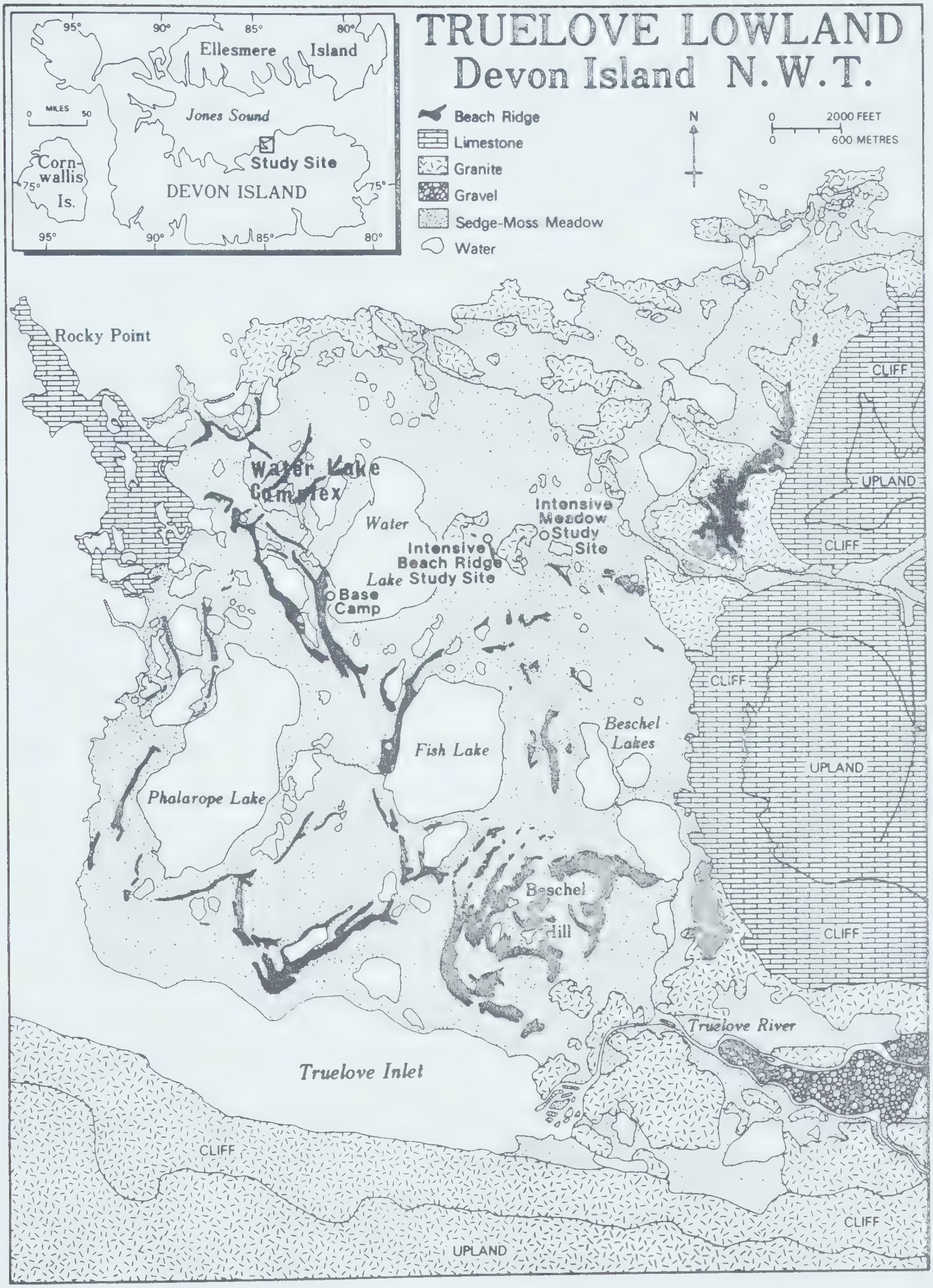

Figure 1. Physiography and local names of Truelove Lowland.

DESCRIPTION OF AREA

The Truelove Lowland (70° 40' N, 84° 40' W) is one of a series of lowlands on the north coast of Devon Island which have emerged from the sea following deglaciation (Barr, 1971). It is bounded on the north and west by Jones Sound, on the east by a dolomitic cliff raising 300 m to an extensive plateau, and on the south by Truelove Inlet and a granitic cliff (Fig. 1). Pleistocene sediments overlaying Precambrian gneisses and Cambrian dolomites (Krupicka, 1972) form the bulk of the Lowland (73%). Precambrian outcrops along the north coast and at the base of the cliff form major relief, ca. 30 m, while a series of raised beach ridges, aged from 3000 to 9500 years (King, 1969) provide minor relief.

Precipitation on the Lowland is largely as snow which accumulated to an average depth of 50 cm in the winter of 1970-71 and 40 cm in the winter of 1971-72 (Muc, 1972, unpublished data). Summer (June-August) precipitation on the Lowland was 65 mm in 1971 and 25 mm in 1972 (Courtin, unpublished data).

Characteristic temperatures on the Lowland are presented in Fig. 2. The isotherms were constructed from hygrothermograph data collected from six micrometeorological stations located along a 5 km transect from Rocky Point to the base of the cliff, and approximate the seasonal temperature changes in 1971 at 15 cm (Courtin, 1972).

Raised beach ridges (15% of Lowland area) are divided into three zones according to vegetation and soil analyses. The crest is characterized by crustose and fruticose lichens (Richardson and Finegan, 1972) with less than 25% vascular plant cover (Svoboda, 1972).

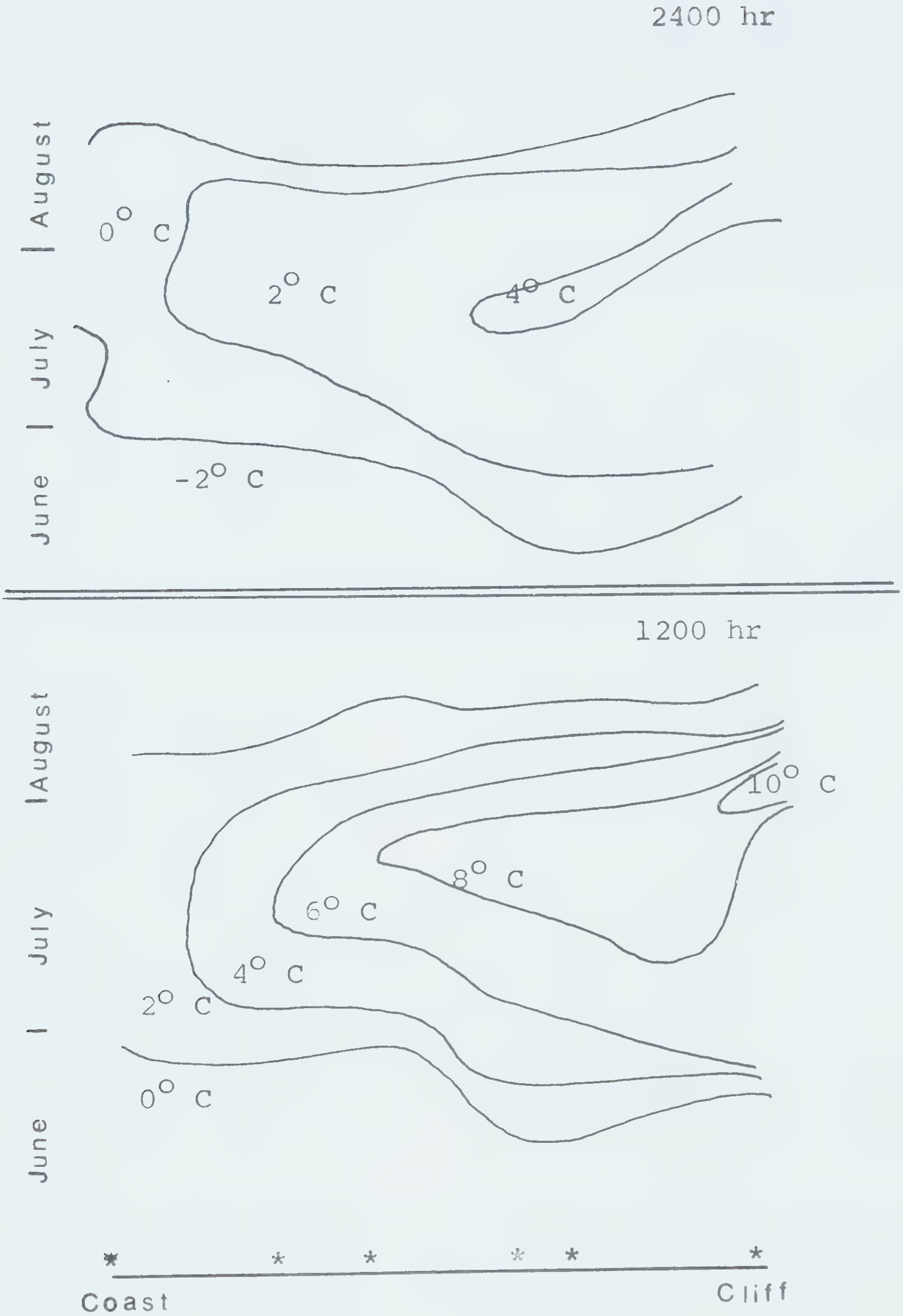

Figure 2. Seasonal isotherms at 15 cm along a 5 km transect from Jones Sound to the dolomitic cliff on Truelove Lowland. Meteorological stations are marked *.

The soil is a Cryic Regosol according to the Canadian classification system (Peters and Walker, 1972). The slope of the beach ridge has 25 to 50% vascular plant cover, and fruticose lichens are relatively more important. Slope soil is a Cryic Eutric Brunisol. At the base of the beach ridge, lichen cover is less important; and vascular plant cover is over 50% (Svoboda, 1972). The soil is a Cryic Rego Glysol (Peters and Walker, 1972).

Meadows (51% of Lowland area) have been segregated into three types: Frost-boil sedge-cottongrass, hummocky sedge-moss, and wet moss-sedge (Muc, 1972). The soils of the three types are similar and have been tentatively classified as Cryic Terric Fibrisol (Peters and Walker, 1972). Hummocky sedge-moss meadows are the most common type, representing 60% of the Lowland meadows. Hummock-depression patterns form important micro-relief, presenting habitat variation for microbes (Widden et al., 1972), invertebrates (Ryan, 1972), and plants (Muc, 1972). These meadows develop in areas of ground water discharge (Table 1).

Frost-boil sedge-cottongrass meadows include 25% of the Lowland meadows and develop in areas of ground water recharge. They tend to have a deeper active layer than hummocky sedge-moss meadows, but are similar in hummock development and are characterized by frost-boil activity.

Wet moss-sedge meadows develop in poorly drained areas as around lakes and along stream beds. These are essentially aquatic habitats with rather uniform soil and vegetation patterns. Hummock development is minor.

Table 1. Physical and biological characteristics of meadows on Truelove Lowland (Muc, unpublished data).

Feature	Frost boil sedge-cottongrass	Hummocky sedge-moss	Wet moss-sedge
Vascular Plant Cover (%)	74	90	77
Bryophyte Cover (%)	74	98	100
Active Layer (cm)	48	27	34
Hummock:Depression	40:60	60:40	-
Frost Boil Development	+	-	-
Hydrology	Ground water recharge	Ground water discharge	Lake side or stream side

MATERIALS AND METHODS

Study Sites

Seven areas including three beach ridges, two hummocky meadows, and two wet meadows were sampled for nitrogen-fixing potential using the acetylene-reduction assay. A beach ridge and hummocky meadow on the east side of Water Lake were chosen as intensive study sites (abbreviated ISS) (Fig. 1). Micrometeorological measurements, soil analyses, and algae collections were taken in these sites.

A beach ridge, a hummocky meadow, and a wet meadow were selected 2 km north-east of ISS and are designated as the Water Lake complex (Fig. 1). A beach ridge near the top of Beschel Hill and a wet meadow 0.5 km south-east of it were selected and designated as the Beschel Hill complex (Fig. 1).

Acetylene reduction

Sampling

Each sample area was defined by three 30 m transects. Six cylindrical soil cores 35 cm^2 (94 mm diameter) x 10 cm were taken at random points along each transect at each sampling time, and were either divided into 0 - 5 cm and 5 - 10 cm segments, or used as single cores. Core depth was measured from the moss surface in meadows and from the soil surface on beach ridges. Each sample consisted of 18 cores. Samples from hummocky meadows were stratified to include 9 cores from hummocks and 9 cores from interhummock areas. In 1971 there were three sample periods, in 1972 sampling was weekly in the intensive study sites and bi-weekly elsewhere.

Incubation

Soil cores were placed intact in 1000 ml or 500 ml incubation jars constructed of Mason jars with modified lids to permit injection and withdrawal of gas samples via syringes (Stutz and Bliss, 1973). The integrity of the seal was tested with a manual vacuum pump. Acetylene, freshly generated from calcium carbide, was injected into each chamber to make 0.1 atms C_2H_2. Throughout the experiment pressure changes due to injection and withdrawal of gas and temperature changes were recognized and accommodated. Control chambers with soil cores but no acetylene were used to monitor natural ethylene evolution. The use of calcium carbide as an acetylene source not only simplified logistic problems, but also provided ethylene-free acetylene, thereby reducing experimental error.

The incubation chambers were placed in a soil pit 10 cm deep and covered with soil to maintain incubation temperatures near those of undisturbed soil. In 1971 and periodically in 1972, soil cores were incubated under standing water so the effects of light on the incubation system could be studied.

Incubation periods of soil cores were relatively long to obtain more accurate estimations of *per diem* reduction rates. In 1971 incubations were 24 hours, in 1972 they were 36 hours. There is no indication prolonged exposure to low concentrations of acetylene is detrimental to nitrogen-fixing organisms, although cell proliferation may be inhibited in some organisms (Brouzes and Knowles, 1973).

Acetylene-reduction rates were determined from changes in ethylene concentration between hours 12 and 36 (or 24). The initial 12 hour delay was to avoid incorporating into the calculations the lag period

in ethylene production and to allow time for a steady state reduction rate to become established (Stutz and Bliss, 1973). The time necessary for a constant rate appears to be related to the moisture regime of the soil (Fig. 3).

Ethylene Determination

Twelve and 36 (or 24) hour samples were withdrawn from the incubation chambers with a disposable syringe and injected into evacuated serum vials into which anhydrous KOH had been placed. The purposes of this were several. Firstly, since gas analysis equipment was in Edmonton, Alberta, a means of preserving and transporting samples had to be provided. Serum vials were easier to ship than entire incubation chambers. Secondly, each chamber could be used for two incubations, i.e., both 12 and 36 hour samples. Many more replications would be necessary if the entire sample was "killed" and transported to Edmonton. Thirdly, there is evidence that "killed" systems are not completely inactivated (Granhall and Selander, 1972), and that non-biological ethylene production may be stimulated by the killing agent (Thake and Rawle, 1972). Fourthly, the KOH in the vial absorbed much of the CO_2 and water, both of which may hinder gas-chromatographic analysis.

Associated with the transfer of gas samples to vials were dilution and leakage factors which were easily accommodated. Figure 4 demonstrates a dilution factor of 75% and a rate of ethylene leakage of 10% in eight weeks.

Ethylene was detected with a Beckman GC-5 gas chromatograph equipped with a hydrogen flame detector. Dual Poropak R columns (100/120 mesh) were used to separate the hydrocarbons in the sample. Carrier gas (nitrogen) flow rate was 120 $ml \cdot min^{-1}$, column temperature was 60° C,

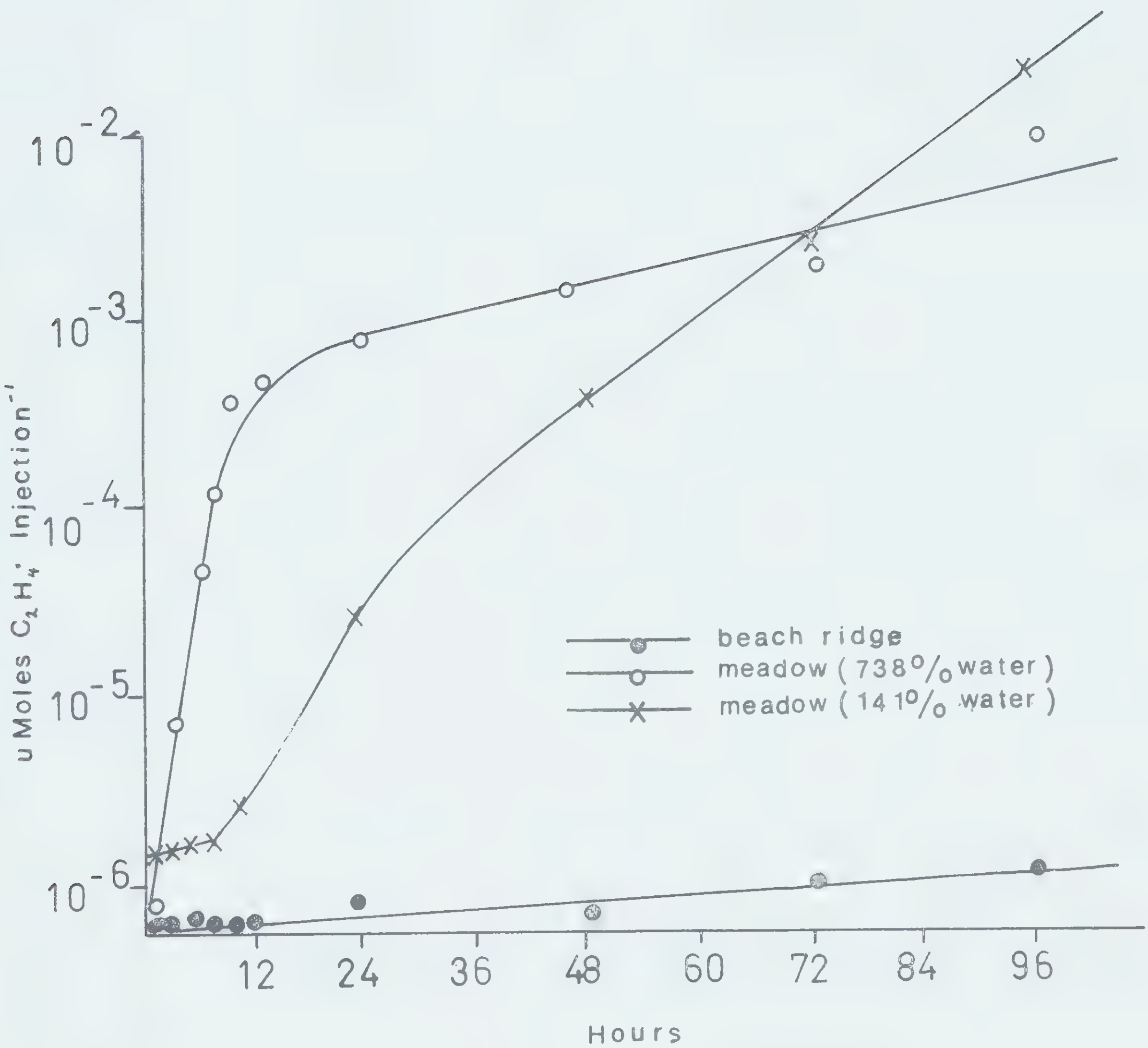

Figure 3. Ethylene accumulation in incubating soil cores exposed to light on Truelove Lowland.

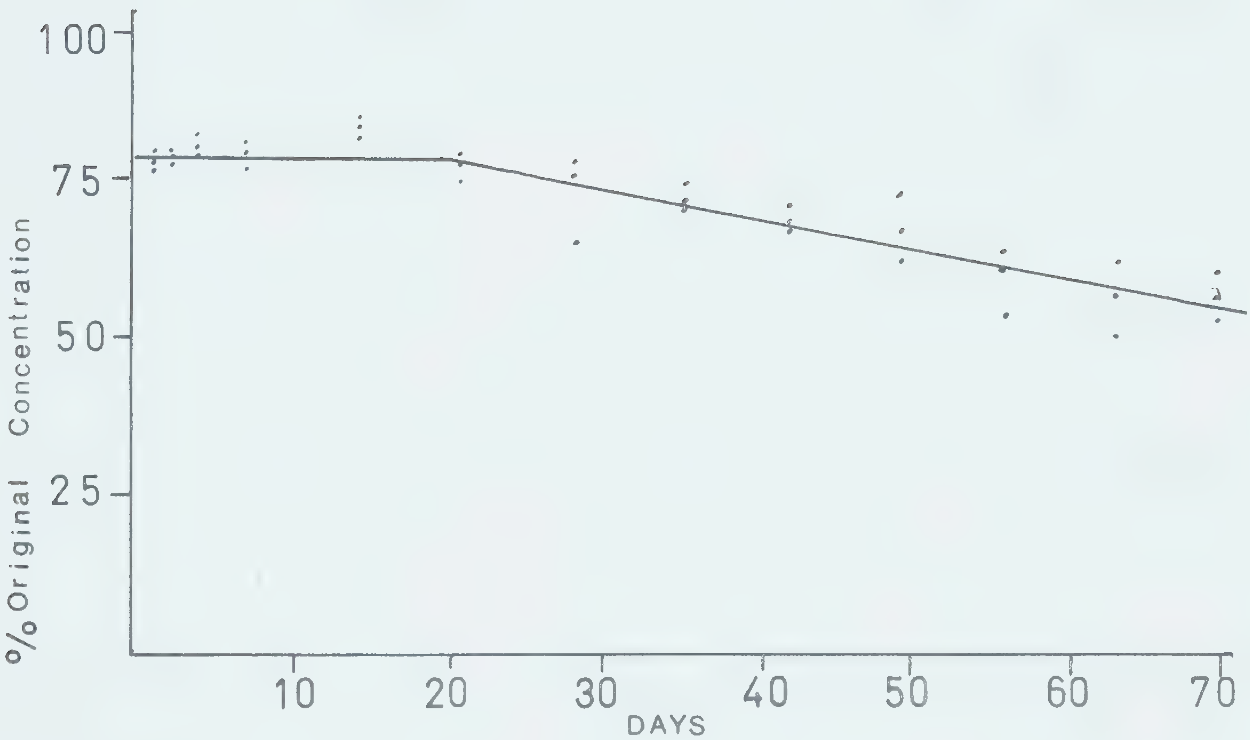

Figure 4. Percent of original ethylene concentration in serum vials as a function of time.

and detector temperature was 95° C. Characteristic retention times were 0.5 min for methane, 1.1 min for ethylene, and 1.3 min for acetylene.

Detector response to methane and ethylene was standardized with commercial analysed gases. Figures 5 and 6 show a log-linear response to ethylene and methane respectively. The system was sensitive to concentrations as low as 10^{-12} moles ethylene$\cdot ml^{-1}$ and 10^{-13} moles methane$\cdot ml^{-1}$. Acetylene was used as an internal standard to detect major defects in procedures.

Soil temperature

Each week an hourly temperature profile was recorded in one of the soil pits at the intensive study sites, and spot readings from the profile of the other site. An Esterline-Angus mv recorder with a stepping switch measured output of copper-constantan thermocouples relative to an ice bath. Five probes were read in sequence twice each hour. The thermocouples were left in place throughout the summer in undisturbed soil at -2 cm and -7 cm, in the soil pit at -5 cm, and in soil cores within incubation chambers (-7 cm) in the pits.

A six probe Yellowsprings (YSI) Telethermometer was used alternatively with the Esterline-Angus system. The thermistors were placed in position the day before the initiation of acetylene-reduction assay to record the same profile. Spot readings were taken during the incubation period by anyone who happened to be in the area. Only once were regular hourly readings maintained for a full incubation period. A restriction of the YSI was that it did not respond to temperatures below 0° C.

Complete temperature data were concurrently being collected by Courtin (1972) at the intensive study sites. The micrometeorological

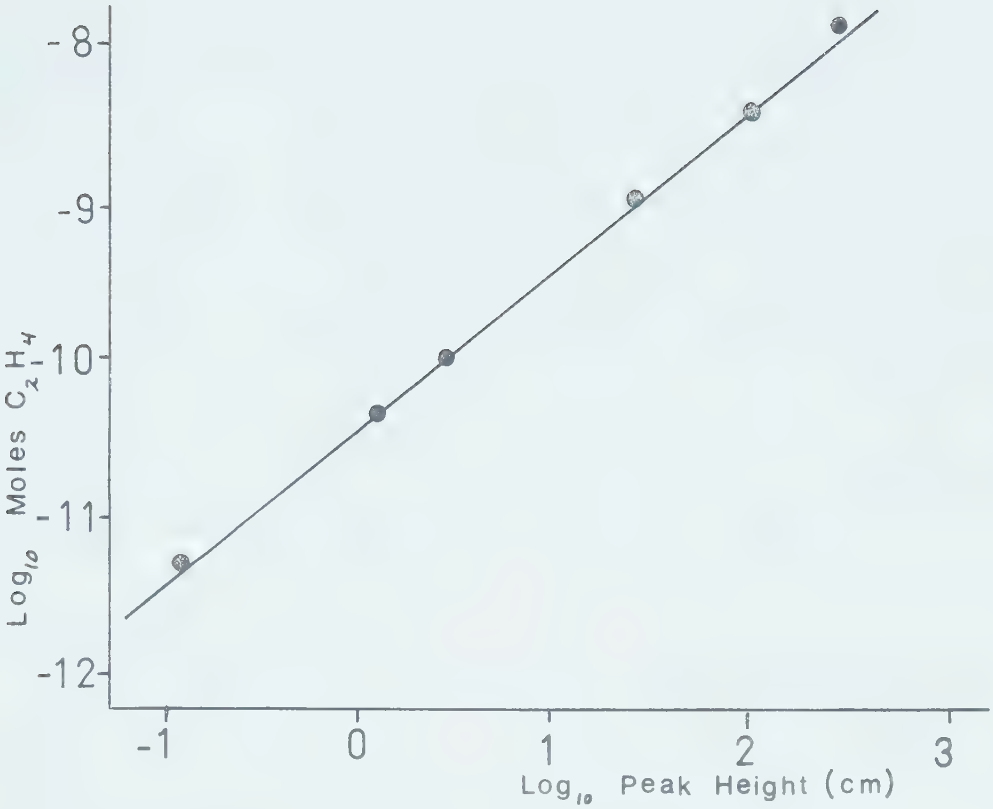

Figure 5. Standard curve of peak height vs. C_2H_4 concentration determined by gas chromatography.

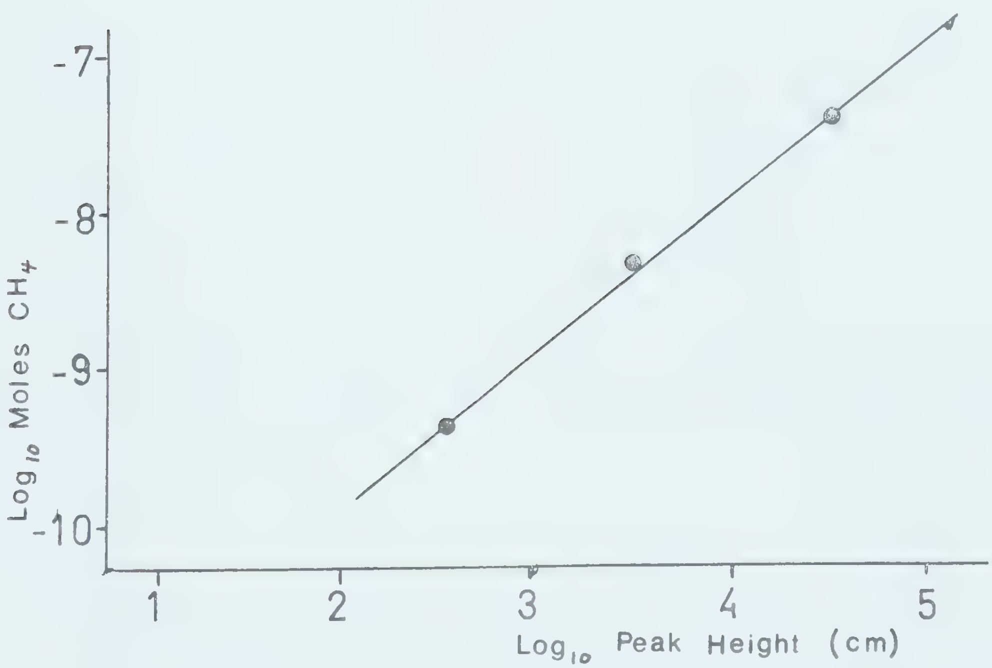

Figure 6. Standard curve of peak height vs. CH_4 concentration determined by gas chromatography.

stations were 15 m from the beach ridge pit and 250 m from the meadow pit.

Temperature data are reported as daily means derived by dividing degree hours above 0° C per day by 24 hours. It is realized that microbial activity may be substantial below 0° C, but this level was used because of the restriction of the YSI temperature unit. Except in very early and very late season, however, soil temperature remained above 0° C so the restriction is of little consequence.

Soil nitrogen

Soil samples were analysed for soluble nitrogen within 6 hours of collection using a steam distillation technique (Bremner, 1965). Soluble nitrogen was extracted by shaking 20 g fresh weight soil samples in 100 ml 6*N* KCl on a reciprocal shaker for 1 hour. The extract (20 ml) was placed in a distillation flask, 5 g MgO were added, and ammonia was distilled over and collected in borate buffer pH 5.8 which was then titrated with normalized 0.005*N* H_2SO_4. Nitrate and nitrite were reduced to ammonia using Devardas' alloy as catalyst and reducing agent. The reduced nitrogen was collected in a second distillation. Data were corrected to oven dry weight (24 hours at 105° C).

A Beckman portable pH meter with a combination probe was used to monitor pH. The procedure was reproducible (± 5%) with nitrogen levels greater than 0.4 ppm.

Soil algae

Nostoc commune, with cartilaginous colonies up to 35 cm in diameter, is a conspicuous component of most meadows. To estimate cover and biomass of this species, two sampling methods were used. Cover percent was estimated by line intercept (Phillips, 1959) of five

20 m transects through each of six meadows. In addition, algal colonies were harvested from 25 randomly placed 2 x 5 dm plots, weighed, and the surface area measured using a photometric leaf-area meter.

Soil was dispersed in a nutritive medium and serial dilutions from 10^{-1} to 10^{-8} g soil$\cdot$ml^{-1} were made in 10 replicates. The cultures were incubated in light at 20° C for 28 days. The number of reproducing units (i.e. cells and colonial fragments) was determined from Most Probable Number tables (Halvorson and Ziegler, 1933). The medium was Bold's Basal Medium (Kantz and Bold, 1969) which is selective for Chlorococcum. Subsequent examination of algal cultures showed that while several algal genera were represented in culture, only Chlorococcum was found in the most dilute cultures.

Relative density estimates of soil algae were obtained by recording the frequency of each algal form encountered in 30 observations (10 fields of vision on 3 microscope slides) of soil-water suspensions. Four frequency classes were recognized: Rare (0 - 5%), occasional (5 - 50%), common (50 - 95%), and abundant (95 - 100%).

Colony size was recorded on a $\log_2$ scale since the relatively mild dispersion technique used in dilution culture was likely to fragment colonies and trichomes, but not completely disperse all cells. Single cell forms and small colonies up to 5 cells were scored 1, colonies with 5 to 20 cells were scored 2, colonies with 20 to 100 cells were scored 4, colonies up to 500 cells were scored 8, and colonies of more than 500 cells were scored 16. The implication of this is that very large colonies would likely fragment into 16 reproducing units when cultured. Density was calculated as the product of

frequency percent and colony size. Density figures from different soils were not comparable since soil-water ratios of the suspensions varied. Relative density--(species density) $\cdot$ (total density)$^{-1}$-- was used as the basis of comparison.

RESULTS AND DISCUSSION

Acetylene-reduction rates

Acetylene-reduction rates of Truelove Lowland meadows measured in 1971 were several times higher than rates measured in 1972 (Table 2). This is due primarily to the different incubation methods used in each season. In 1971 incubations were exposed to light while in 1972 they were routinely covered by soil. Figure 7 presents results from the replications in 1972 which were exposed to light. The difference between reduction rates under the two incubation conditions may be considered a function of temperature differences, changes in aeration in the incubation jars, and nitrogen-fixation by algae which depend on photosynthesis for energy.

The maximum rate of acetylene-reduction in meadows was 7.5 umoles$\cdot m^{-2} \cdot hr^{-1}$ in 1971 and 2.4 umoles$\cdot m^{-2} \cdot hr^{-1}$ in 1972 (Table 2). These rates are comparable to rates measured at Point Barrow, Alaska where rates of acetylene-reduction were as high as 6 umoles$\cdot m^{-2} \cdot hr^{-1}$ in soil samples exposed to light (Alexander *et al.*, 1970). Grassland soils show almost no asymbiotic acetylene-reduction when dry. In southern Saskatchewan soils wetted to field capacity, reduction was 0.16 umoles$\cdot m^{-2} \cdot hr^{-1}$ (Rice, 1970).

Peat lands tend to have a much higher rate of acetylene-reduction. In Great Britain, they show acetylene-reduction rates as high as 23 umoles$\cdot m^{-2} \cdot hr^{-1}$ (assuming 150.0 kg soil$\cdot m^{-2}$ to 5 cm depth) (Waughman and Bellamy, 1972). Swedish peat lands have rates between 1.3 and 2700 umoles$\cdot m^{-2} \cdot hr^{-1}$ (assuming 50 kg moss$\cdot m^{-2}$ to 5 cm depth) in moss samples exposed to light (Granhall and Selander, 1972).

Table 2. Acetylene-reduction rates of meadow soils on Truelove Lowland.

Date	Sample Size	Meadow*	umoles Acetylene.m^{-2}.hr^{-1} 0-10 cm	0-5 cm	5-10 cm
10 July, 1971	10	Water Lake (wet)	1.87		
		ISS (hummocky)	5.18		
		ISS (frost boil)	7.53		
13 Aug., 1971	7	Beschel (wet)	0.30		
		Water Lake (wet)	0.86		
		Beschel (hummocky)	2.47		
		Water Lake (hummocky)	2.61		
12 July, 1972	15	Water Lake (wet)		0.00	0.00
		Water Lake (hummocky)		0.00	0.00
		Beschel (wet)		0.41	0.00
		ISS (hummocky)		0.91	0.12
24 July, 1972	15	Water Lake (wet)		0.31	0.00
		Water Lake (hummocky)		0.79	0.01
		Beschel (wet)		0.97	0.05
		ISS (hummocky)		2.21	0.23
6 Aug., 1972	15	Water Lake (wet)		0.72	0.00
		Beschel (wet)		0.83	0.00
		Water Lake (hummocky)		1.26	0.10
		ISS (hummocky)		2.35	0.26

*Areas not scored by the same vertical line are significantly different by Duncans Multiple Range Test. P = 0.95. Soils were incubated in the light in 1971 and in the dark in 1972.

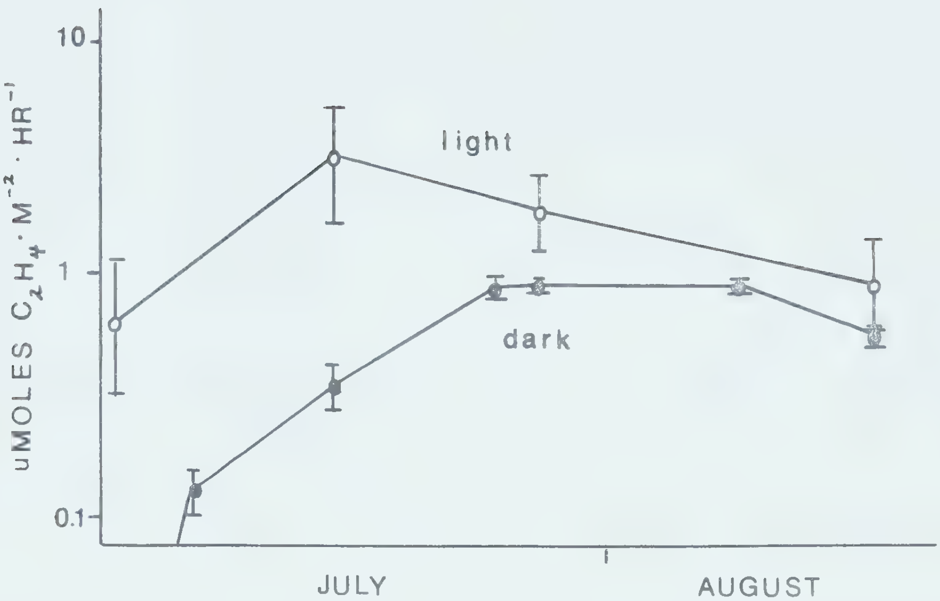

Figure 7. The effect of light on ethylene production of meadow soil cores from Truelove Lowland, 1972.

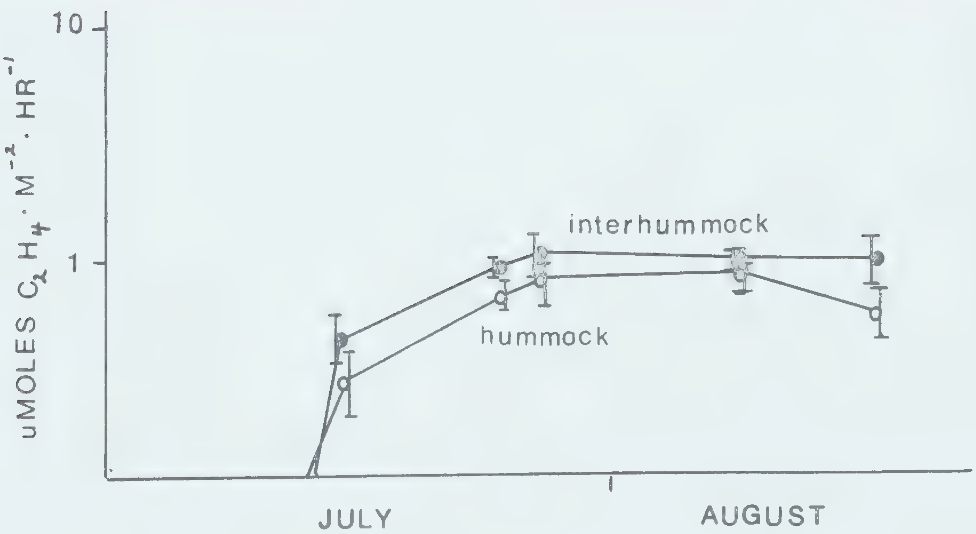

Figure 8. Acetylene reduction rates in soil from hummocky meadow, 1972.

On Truelove Lowland, differences between hummock and interhummock acetylene-reduction rates are evident only in mid-season. Generally mean values for acetylene-reduction in interhummock areas were higher than on hummocks, but variation between replications was larger than the difference in most cases (Fig. 8).

The rate of acetylene-reduction on beach ridges was an order of magnitude below that of hummocky meadows (Table 3). Beschel Hill showed nitrogenase activity several weeks before beach ridges in other areas because this area was much warmer in spring than the Lowland in general (Courtin, 1972). For most of the season, however, beach ridges in all parts of the Lowland showed similar reduction rates.

Mean reduction rates of light-incubated samples from beach ridges tended to be higher than dark-incubated samples although the effect was less than with meadow soils.

Environmental factors affecting acetylene-reduction

Temperature

Biological processes change exponentially with temperature, the rate of change often expressed as Q_{10}.* In simple systems, Q_{10} varies between 1 and 3, but under field conditions there are so many interacting factors, both physical and biological, responding to temperature that the effect of temperature on a process may be greatly amplified. For example, Hardy et al. (1968) show data from which a Q_{10} of 8.8 can be calculated between 10° and 15° C for acetylene-reduction in soybean.

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* $$Q_{10} = \left(\frac{k_2}{k_1}\right)^{\frac{t_2-t_1}{10}}$$ where k_1 = rate at temp. t_1 and k_2 = rate at temp. t_2 (Salisbury and Ross, 1969)

Table 3. Acetylene-reduction rates of beach ridge soils on Truelove Lowland.

Date	Sample Size	Location*	umoles Acetylene$\cdot m^{-2} \cdot hr^{-1}$ (0-10 cm)
14 June, 1971	17	Beschel Hill	0.23
10 July, 1971	25	Beschel Hill	0.40
		ISS	0.72
13 Aug., 1971	37	Water Lake	2.63
		ISS	3.18
20 June, 1972	15	ISS	0.00
		Water Lake	0.00
		Beschel Hill	0.13
6 July, 1972	9	ISS	0.02
		Water Lake	0.03
		Beschel Hill	0.08
12 July, 1972	15	Beschel Hill	0.08
		Water Lake	0.13
		ISS	0.14
24 July, 1972	15	ISS	0.13
		Water Lake	0.15
		Beschel Hill	0.16
6 Aug., 1972	15	Beschel Hill	0.10
		ISS	0.41
		Water Lake	1.10

* Areas not scored by the same vertical line are significantly different by Duncans Multiple Range test. P = 0.95. Soils were incubated in the light in 1971 and in the dark in 1972.

Nephroma arcticum and Solorina crocea from Finland show an acetylene-reduction Q_{10} of 9.6 and 4.4 respectively between 5° and 10° C (Kallio et al., 1972).

An experiment in which 18 soil cores selected for uniformity from the intensive study site meadow were incubated under two temperature regimes was used to estimate the effect of temperature on acetylene-reduction in the Lowland. One group of 9 cores was incubated in the meadow soil pit which had a 24 hour mean temperature of 4.7° C (range 2.6° to 5.2° C), the other group in the beach ridge soil pit which had a 24 hour mean temperature of 1.9° C (range 0.0° to 4.8° C). Acetylene-reduction was 145 $\pm$ 20 uumoles·g soil^{-1}·hr^{-1} in the meadow and 90 $\pm$ 8 uumoles·g soil^{-1}·hr^{-1} in the beach ridge; 1.6 fold increase in rate with 2.8° C rise in temperature or an apparent Q_{10} of 5.6.

With regard to incubation conditions, temperatures of light and dark incubations differed markedly. Temperatures of dark-incubated soil cores closely resembled those of soil at -7 cm. There was relatively small diurnal and seasonal variation, and generally temperatures remained below 10° C (more so in wet than dry soils). Temperatures of soil cores exposed to light showed much greater diurnal fluctuation, even more than the water under which they were incubated (Fig. 9), and were often much higher than temperatures of dark-incubated cores. Acetylene-reduction rates of soil cores were thereby affected.

Aeration

The effect of aeration on nitrogen-fixation has been extensively studied in many systems. Asymbiotic nitrogen-fixation in soils achieves maximum rates with periodic flooding (Barrow and Jenkinson, 1962). Magdoff and Bouldin (1970) present evidence that nitrogen-fixation is greatest

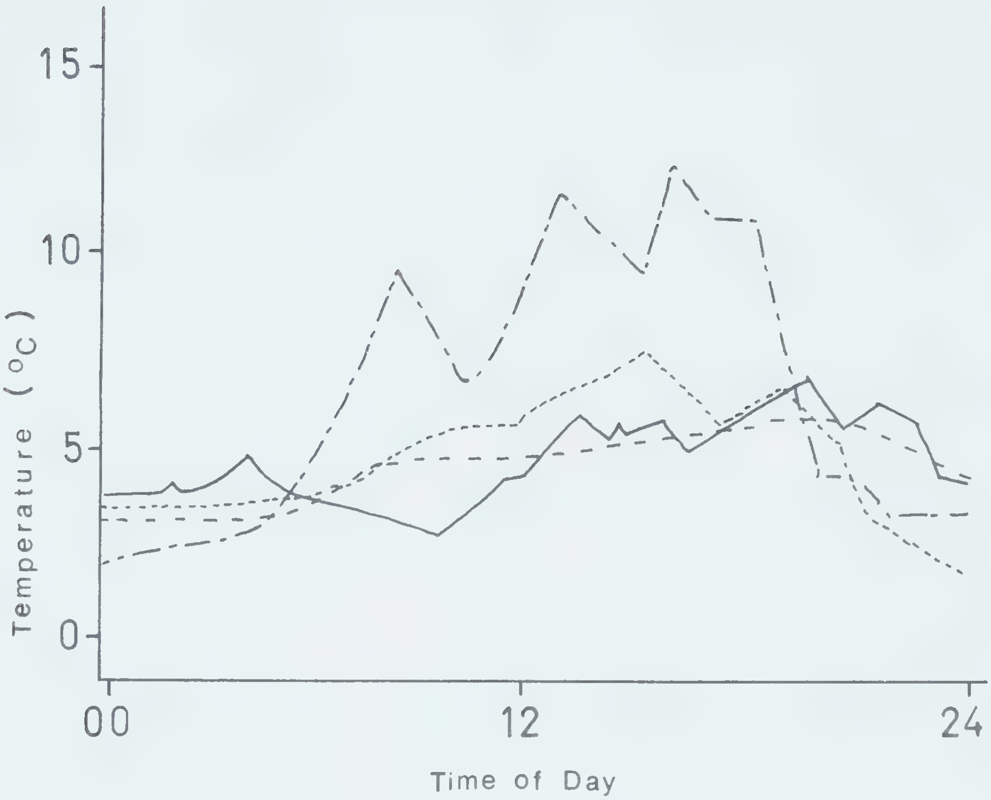
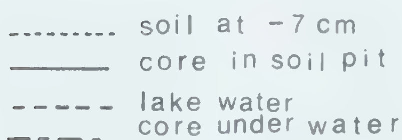


Figure 9. Incubation temperatures of soil cores in soil pits and under standing water. 8 August, 1971.



at the interface between anaerobic and aerobic conditions in water-logged soils. It has been suggested that anaerobes and aerobes act symbiotically in nitrogen-fixation, one group of organisms fixing nitrogen using as an energy source the metabolic products of the other group (Jensen, 1941; Vartiovaara, 1938). Rice (1970) demonstrated more rapid acetylene-reduction in aerobic soil-straw incubations when straw was the only energy source, but when glucose was added to the system anaerobic acetylene-reduction was very much more rapid. These data were interpreted as showing the dependance of anaerobic nitrogen-fixing bacteria (Clostridium) on aerobic cellulose-decomposing organisms for an energy substrate.

On Truelove Lowland there is evidence of accelerated nitrogen-fixing activity at the anaerobic-aerobic interface. Hummocky meadows, which have an extensive aerobic-anaerobic interface show the highest acetylene-reduction rates of any habitat (Table 2). Similarly, as the water table dropped over the season, the importance of the 5 to 10 cm segment of the soil profile increased as a nitrogen-fixation zone in hummocky meadows, reflecting the subsidence of this biologic interface.

Wet meadows on the Lowland are perpetually water-logged, i.e., anaerobic conditions prevail. Methane was detected in large amounts in these meadows (Fig. 10) indicating activity of anaerobic microflora. In wet meadows acetylene-reduction was an order of magnitude below that in hummocky meadows. Beach ridge soils are so well drained they also lack well-developed interface between aerobic and anaerobic conditions. In these habitats acetylene-reduction rates are similar to those of wet meadows (compare Tables 2 and 3).

The effect of aerobic-anaerobic interface on acetylene-reduction can be seen by comparing rates of acetylene-reduction measured under

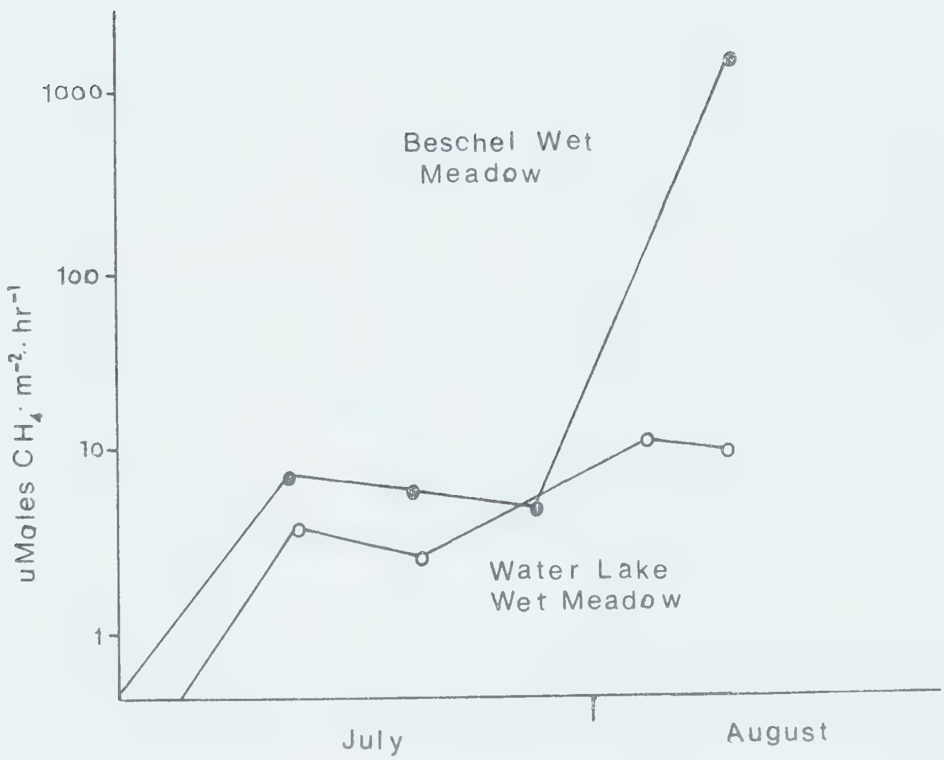


Figure 10. Methane evolution from incubating soil cores taken from Truelove Lowland meadows. 1972.

light and dark conditions. Figure 11 plots the rate of acetylene-reduction in meadow soil with time under the two light regimes. While the incubation exposed to light soon achieved a stable rate, dark incubated soil cores showed continuous decrease in reduction rate. Beach ridge soil, whether incubated in light or dark, maintained a constant acetylene-reduction rate.

The oxygen regime of meadow soil cores, because of their high water content, was significantly altered when they were removed from the ground. As anaerobic conditions were re-established via microbial respiration, acetylene-reduction increased, hence the increase in rate for the initial 12 hours. Photosynthetic organisms maintained an aerobic phase in the light and acetylene-reduction remained near the maximum rate. In the dark, however, anaerobiosis became more important and acetylene-reduction rate continually decreased. Algal populations on the order of 10^5 cells.g soil^{-1} (Table 13) probably contributed much to the oxygen regime of light-incubated chambers, as well as the more conspicuous mosses and vascular plants. Carbon dioxide flux from denuded soil on the hummocky meadow was significantly negative (net photosynthesis was positive) according to infra-red gas analysis (J. Mayo, personal communication).

Soluble Nitrogen

Various researchers have reported inhibitory effects of even small amounts of ammonium and nitrate on nitrogen-fixation by cultures of <u>Azotobacter</u>, <u>Clostridium</u>, etc. (cf. Burris, 1968). Cell-free enzyme preparations are not inhibited by inorganic nitrogen, however, suggesting ammonium and nitrate are repressors of nitrogenase synthesis rather than inhibitors of enzyme activity (Strandberg and Wilson, 1968).

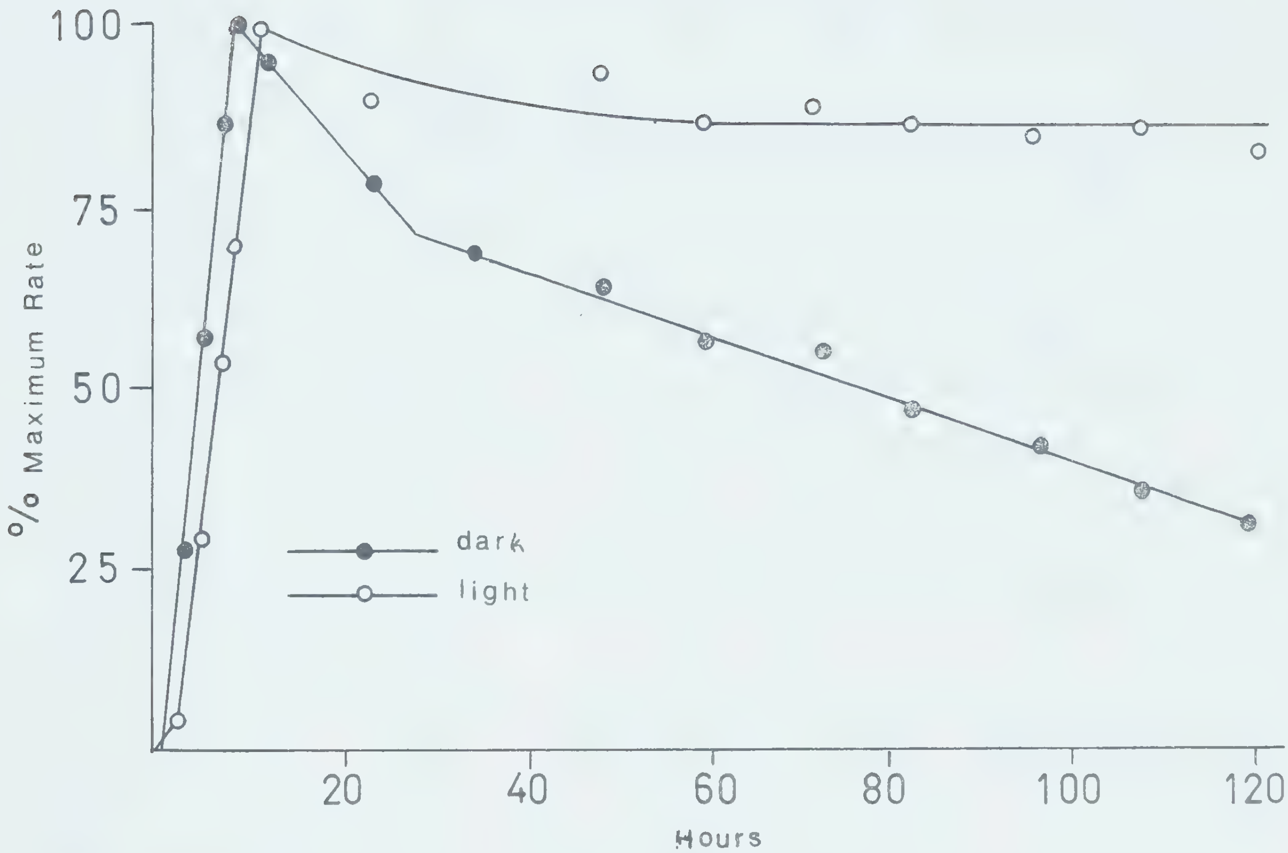


Figure 11. Rate of acetylene reduction vs. time for incubations exposed to light and incubations kept in the dark. 24 July, 1972.

Few data on the effect of inorganic nitrogen on nitrogen-fixation under natural conditions are available. Rice (1970) showed 95 and 84% inhibition of asymbiotic acetylene-reduction when 500 ug nitrogen was added to 2 g soil-straw mixture as ammonium and nitrate respectively.

Analysis of KCl-extractable nitrogen in Truelove Lowland soils showed as much as 10 ppm NH_4^+-N on meadow hummocks, but only 2 ppm elsewhere (Table 4). No nitrate was detected in freshly extracted soils, but nitrate accumulated in soils sent to Edmonton for analysis, sometimes as much as 40 ppm (Peters and Walker, 1972). Nitrifying organisms are probably present in the soil, but their activity is generally so low, nitrate does not accumulate. Low rates of nitrification are generally characteristic of climax ecosystems (Rice and Pancholy, 1972).

The absence of detectable nitrate in the soil afforded the opportunity to assess the effects of soluble nitrogen on acetylene-reduction. Replicate soil samples from a hummocky meadow were placed in incubation jars with either 10 ml water or 10 ml solution containing 118 mg $Ca(NO_3)_2 \cdot l^{-1}$ (20 ug $N \cdot ml^{-1}$) and incubated in the dark for 36 hours. Subsequent analysis of the soil showed 1 ppm NO_3^--N (Table 5). Acetylene-reduction rate was 2.34 ± 0.15 $umoles \cdot m^{-2} \cdot hr^{-1}$ in controls and 1.32 ± 0.20 $umoles \cdot m^{-2} \cdot hr^{-1}$ in the treated samples, 56% inhibition with 38% increase in soluble nitrogen. These data suggest nitrogenase is extremely labile under incubation conditions. Acetylene-reduction rates therefore may reflect the rate at which the enzyme is synthesized which is a function of population size and activity of acetylene-reducing organisms. Nitrogenase activity associated with inactive organisms is nil.

Table 4. Soil analysis for ammonium and nitrate nitrogen in beach ridge and hummocky meadow soils on Truelove Lowland, 1972.

Date	ppm Nitrogen					
	Beach ridge		Hummocks		Interhummock	
	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-
1 July	-	-	4.5	0.0	1.4	0.0
15 July	2.0	0.0	8.4	0.0	1.7	0.0
1 August	0.5	0.0	3.3	0.0	2.3	0.0
15 August	1.6	0.0	9.6	0.0	3.4	0.0

Table 5. Soil analysis for ammonium and nitrate nitrogen in hummocky meadow soil used for acetylene-reduction assays 20 July, 1972. Nitrate was added as $Ca(NO_3)_2$.

Core Number	Treatment	ppm Nitrogen	
		NH_4^+	NO_3^-
1	Control	2.4	0.0
2	Control	1.8	0.0
3	Control	1.5	0.0
4	Control	2.0	0.0
5	Control	0.9	0.0
6	Control	2.2	0.0
7	NO_3 added	2.9	0.5
8	NO_3 added	3.1	1.3
9	NO_3 added	1.2	0.5
10	NO_3 added	2.3	1.1
11	NO_3 added	1.9	0.7
12	NO_3 added	2.2	1.1

Whether the KCl extract contains all the ammonium available to nitrogen-fixing organisms is doubtful. Replicate soil samples extracted with KCl before and after being dried at 105° C for 24 hours differed significantly. As much as 150 ppm NH_4^+-N was extracted from dried soil (Table 6). The nature and ecological significance of the heat-labile ammonium bond has not been investigated.

The origin of ammonium in soil is not yet clearly understood. There is evidence that ammonium in soil is not the product of extra-cellular microbial metabolism. While fungi and bacteria secrete digestive enzymes (Pollock, 1960), they have not been shown to secrete deaminases which are necessary for ammonification. Deaminations are generally oxidative rather than hydrolytic. Considerations of the effects of enzyme concentration, substrate concentration, the enormous fluctuations in chemical and physical properties of soil, and the requirement of enzymatic oxidations for prosthetic groups suggest that oxidative deamination is effective only intracellularly (Dixon and Webb, 1964). Consequently, amino acid decomposition in soils proceeds without accumulation of extracellular intermediates (Greenwood and Lees, 1960), the amino acids often being incorporated into microbial protoplasm with no alteration (Stokes and Bayne, 1961). Micro-organisms may excrete small amounts of amino acid, ca. 1% of their total nitrogen when nutrients and energy are unlimited (Roberts et al., 1957; Naguib et al., 1972), but are generally nitrogen thrifty (Valdkamp, 1968).

On the other hand, it has been shown that animals excrete nitrogenous wastes in the form of ammonia, urea, uric acid, allantoic acid, etc. The soil fauna is perhaps responsible for ammonification more so than the soil flora. Table 7 gives estimated populations and

Table 6. Concentration of KCl-extractable nitrogen in soils from Truelove Lowland before and after they were dried at 105° C. 8 Aug., 1972.

Soil	Depth (cm)	ppm NH_4^+-N* Fresh	Dried
Beach ridge	0- 5	0.3	14.3
	5-10	0.4	6.6
Beach ridge	0- 5	0.8	12.7
	5-10	0.8	5.0
Inter-hummock	0- 5	2.3	47.6
Meadow hummock	0- 5	3.3	164.0

*No nitrate was detected in the soil.

activities of soil invertebrates in meadow soil on Truelove Lowland (Ryan, 1972). As nitrogenous wastes, protozoa excrete ammonia (Kitching, 1967), nematodes ammonia and urea (Rogers, 1969), and enchytrids and copepods ammonia and urea (Schoffeniels and Gilles, 1970). While adult insects generally excrete uric acid, aquatic forms such as dipteran larvae excrete ammonia (Bursell, 1967). Vertebrate herbivores also contribute to ammonification of the Lowland, but to a lesser degree because of their relatively low biomass, e.g., Muskoxen--3×10^{-2} $g{\cdot}m^{-2}$(Hubert, 1972); Lemming--4.6×10^{-4} $g{\cdot}m^{-2}$ (Speller, 1972).

Biological agents of acetylene-reduction

Nitrogen-fixation can be accomplished by symbiotic bacteria, lichens, blue-green algae, and free-living bacteria. It is not yet possible to quantify the role each group plays in nitrogen-fixation on Truelove Lowland, but there are data available to indicate the relative importance of each group.

Symbiotic nitrogen-fixation by vascular plants is not apparent on the Lowland. Plants commonly associated with nitrogen-fixation, e.g., Leguminosae and Alnus, are absent. Conspicuous nitrogen-fixing nodules have been reported on Dryas integrifolia roots in Alaska (Lawrence et al., 1967), and on Disco Island (M. Lewis, personal communication), but were not seen on the plants growing on Truelove Lowland, even though numerous observations of roots were made throughout three growing seasons. Alexander et al. (1970) reported acetylene-reduction by a variety of vascular plants, but did not demonstrate the effect was symbiotic rather than rhizosphere effect on free-living microbes (Harris and Dart, 1973).

Table 7. Biomass of soil invertebrates in meadows on Truelove Lowland (Ryan, 1972).

Taxon	Biomass ($g \cdot m^{-2}$)	Production ($g \cdot m^{-2} \cdot yr^{-1}$)	Primary Food
Protozoa	0.1	1.5	bacteria
Nematodes	0.5	1.5	bacteria, fungi
Enchytrids	2.5	1.25	fungi
Copepods	0.1	0.2	protozoa
Insecta			
Collembola	0.5	0.05	fungi
Diptera	0.3	0.16	detritus

Blue-green algae are active nitrogen-fixers in association with lichens either as symbionts or as cephalodia (Hale, 1967). While lichens account for about 50% ground cover on beach ridges (Richardson and Finegan, 1972) and are present in other habitats on Truelove Lowland, few species are capable of nitrogen-fixation. Table 8 lists the species which were tested for acetylene-reduction. Of these species, blue-green algae are absent in all but Peltigera aphthosa on which Nostoc initiates cephalodia (thallus outgrowths containing a non-phycobiont alga). Peltigera aphthosa reduced acetylene at a rate of 5.1 uumoles$\cdot$mg$^{-1}\cdot$hr^{-1}. None of the other species showed positive results.

The rate of acetylene-reduction of P. aphthosa is comparable to the rate measured for the species in Alaska (Alexander et al., 1970) and 10% of the rate measured in a Swedish bog (Granhall and Selander, 1972). Acetylene-reduction has been reported in species of Thamnolia (Alexander et al., 1970), Stereocaulon (Lid and Hansen, 1972), and Umbilicaria (Granhall and Selander, 1972), although bacteria rather than algae are reported to be the agents of reduction in the latter case.

Blue-green algae are important nitrogen-fixers in desert (Cameron and Fuller, 1970), grassland (Paul et al., 1972), peatland (Granhall, 1970), arctic (Alexander et al., 1970), and Antarctic (Cameron and Devany, 1970) ecosystems. On Truelove Lowland Nostoc commune forms a prominant feature of meadows. Its biomass was estimated as high as 39 mg$\cdot$m^{-2} in favorable habitats, averaging 17 mg$\cdot$m^{-2} in mesic meadows and 9 mg$\cdot$m^{-2} in wet meadows (Table 9).

Table 10 shows the results of several assays for acetylene-reduction in Nostoc commune rates in general 5 to 10 times that of

Table 8. Species list of lichens from Truelove Lowland tested for acetylene-reduction. 20 July, 1972. Results are the mean of triplicate assays.

Species	Habitat	uumoles ethylene. $mg^{-1}.hr^{-1}$
Cetraria ericator	Beach ridge	-
C. nivalis	Beach ridge	-
Dactylina arctica	Meadows	-
Parmelia rudecta	Beach ridge	-
Peltigera aphthosa	Meadows	5.1
Pertusaria dactylina	Beach ridge	-
Rhizocarpon geographicum	Beach ridge	-
Stereocaulon alpinum	Beach ridge	-
Thamnolia vermicularis	Beach ridge	-
Umbilicaria lyngic	Beach ridge	-
Xanthoria elegans	Meadows	-

Table 9. Cover and biomass of Nostoc commune as determined by two sample methods.

Meadow	Line intercept Cover %	$mg \cdot m^{-2}$ *	2 x 5 dm Plots Cover %	$mg \cdot m^{-2}$
ISS Hummocky	1.0	9.0	1.9	17.1
ISS Frost boil	0.03	0.3	1.0	9.2
Beschel Hill Hummocky	1.5	13.5	4.3	38.6
Beschel Hill Wet	0.7	6.3	0.7	0.5
Water Lake Hummocky	2.9	26.1	3.1	29.2
Water Lake Wet	1.2	10.8	-	-

*100 cm^2 algae weighs 90.1 ± 3.4 mg.

Table 10. Acetylene-reduction by Nostoc commune.

Date	Conditions	Mean incubation temperature (° C)	uumoles $C_2H_4 \cdot mg^{-1} \cdot hr^{-1}$
July, 1971	Field	?	6.2
Sept., 1971	Growth Chamber	0.5	33.4
Sept., 1971	Growth Chamber	5.5	53.0
July, 1972	Field	5.0	44.0
July, 1972	Field	12.0	22.8

Peltigera aphthosa. On the basis of replicates in a growth chamber, a Q_{10} of 3.3 can be calculated. On the basis of field incubations, it appears that the optimum temperature for acetylene-reduction is below 12° C.

In addition to macroscopic colonial forms, soils of the Lowlands have numerous epiphytic and free-living blue-green algae (Table 11). The lack of soil algae enumerations reported in the literature is a reflection on the difficulty of obtaining such figures rather than an unawareness of their importance. It is difficult to develop a culture medium (or even a series of media) which will support all algal taxa equally well. Inevitably fast-growing forms will mask slow-growing forms, and certain groups will fail to grow at all. The criterion for determining which medium to use is often based on which media will yield the highest counts (Cullimore and McCann, 1972).

Soil algae enumerations based entirely on culture techniques have an additional potential for error in that dormant algal forms in the soil may reactivate in culture.

While direct microscopical observations of soil particles may yield a more accurate estimation of species composition, the technique is far too time consuming to be accommodated in this type of study. Furthermore, the accuracy of an enumeration may be restricted by gross variation in colonial size and habitat selection from one species to another.

Soil algae on Truelove Lowland soils were enumerated using a combination of culture and direct observation techniques. Soil-water suspensions were examined and the relative density of each algal form was recorded. This gave some notion of relative population dynamics

Table 11. Algae genera observed in soil-water suspensions on Truelove Lowland in 1972.

Chlamydomonadaceae	Chroococcaceae
Chlamydomonas	*Aphanothece*
	Gleocapsa
Chlorococcaceae	*Gleothece*
Chlorococcus	
	Dermatocarpaceae
Desmidaceae*	*Dermocarpa*
Cosmarium	
	Nostocaceae
Microsporaceae	*Anabaena*
Microspora	*Nodularia*
	Nostoc
Protococcaceae	
Protococcus	Oscillatoriaceae
	Oscillatoria
Ulothrichaceae	
Hormidium	Rivulariaceae
	Calothrix
Zygnemataceae	
Mougeotia	Scytonemataceae
	Microchaete
Tabellariaceae	*Scytonema*
Diatomella	
Naviculaceae	
Amphiprora	
Gyrosigma	
Navicula	
Pinnularia	

*For Desmid flora of Truelove Lowland see Croasdale, 1965.

over the growing season. Relative density data were compared with a genus for which an accurate count was obtained by dilution culture techniques. Chlorococcum was chosen as the reference genus because it was a major component of the soil flora in early spring, and because a well-defined, selective medium had been developed (Kantz and Bold, 1969). Having information on the numbers of Chlorococcum in the soil (Table 12) and on the contribution of this genus to the total algal flora (Table 13), the total algal population can be extracted. The relative densities of the other algal groups permit an estimate of their population (Table 13).

Algal populations were as high as 10^5 cells$\cdot$g soil^{-1} (Table 13). This is within the range found in tundra soils in the USSR (Gromov, 1956) and in Alaska (Cameron, 1972).

As with arctic soil in USSR (Novichkova-Ivanova, 1971), soils on Truelove Lowland were dominated by Cyanophyta which usually provided 75 to 95% of the soil algae biomass. Heterococcales was not as strongly represented in Lowland soils as in Russian soils (Novichkova-Ivanova, 1963).

Of the algal flora, members of Nostocaceae, Rivulariaceae, and Scytonemataceae have been shown to fix nitrogen (Shields and Durrell, 1964). Nostoc, sp. is the most abundant form in both beach ridge and meadow soils, composing as much as 85% of the algal flora. The population of this group in interhummock areas of hummocky meadows was maximum in mid-July with 4.3×10^5 cells$\cdot$g soil^{-1}. Calothrix (Rivulariaceae) was observed only sporadically in meadow soils and was never an important component. Scytonemataceae, detected only in inter-hummock areas, was usually unimportant except in late July when a

Table 12. Population of Chlorococcum spp. in different soils on Truelove Lowland as determined by dilution culture. Samples were taken in 1972 and were incubated in Bold's Basal Medium at 20° C for 28 days. Number of cells per gram air dry soil was taken from Most Probable Number tables.

Habitat		number·g soil^{-1} (air dry wt.) 1 July	20 July	1 August
Beach Ridge				
Crest	0-2 cm	2.5×10	0.0	0.0
Slope	0-2 cm	9.3×10^2	2.0×10^3	10
Hummocky Meadow				
Hummock	0-2 cm	6.0×10	1.2×10^4	10
	2-5 cm	-	1.5×10^2	-
Interhummock	0-2 cm	1.5×10^2	5.0×10^3	1.0×10^3
	2-5 cm	10	-	-
Wet Meadow	0-2 cm	-	3.0×10^3	-
Frost Boil	0-2 cm	10	-	0.0

Table 13. Relative density expressed as percent of algal families in soils on Truelove Lowland as determined by direct observation of fresh soil samples, 1972.

		% of Total Algal Density								
Habitat	Date	Chlorococcaceae	Desmidaceae	Protococcaceae	Naviculariaceae	Chroococcaceae	Nostocaceae	Oscillatoriaceae	Scytonemataceae	Total # cells/g soil
Beach Ridge Crest	16 July	5.2	9.3	-	-	-	85.5	-	-	1.9×10^1
	8 Aug.	0.5	-	-	-	23.6	10.7	65.2	-	2.0×10^1
Beach Ridge Slope	11 July	1.4	-	0.4	0.2	35.4	62.3	0.2	-	9.3×10^4
	16 July	26.1	-	13.0	30.4	13.0	17.1	0.4	-	7.3×10^3
	8 Aug.	0.8	-	-	0.2	36.5	61.5	0.9	-	1.2×10^3

Table 13. (Continued)

Habitat	Date	% of Total Algal Density								Total # cells/g soil
		Chlorococcaceae	Desmidaceae	Protococcaceae	Naviculariaceae	Chroococcaceae	Nostocaceae	Oscillatoriaceae	Scytonemataceae	
Meadow	20 July	3.1	-	-	-	-	96.9	-	-	5.0×10^4
Hummock	26 July	0.1	-	-	-	11.3	50.0	38.6	-	-
	1 Aug.	0.2	-	0.2	12.3	50.1	37.2	-	-	1.0×10^4
	19 Aug.	0.1	-	-	0.2	37.2	60.4	2.1	-	-
Meadow	20 July	-	-	-	9.3	3.1	86.4	0.3	0.9	5.0×10^5
Interhummock	23 July	0.1	-	-	25.4	42.0	32.5	-	0.1	-
	26 July	0.9	-	-	5.8	36.8	34.2	19.3	3.0	-
	3 Aug.	0.2	-	-	8.3	40.8	30.0	20.7	-	5.0×10^4
	8 Aug.	0.6	-	-	12.9	20.6	32.3	33.6	-	-

population of 4.5×10^3 cells$\cdot$g soil^{-1} was measured.

The importance of blue-green algae as nitrogen-fixers was assessed by calculating acetylene-reduction rates based on temperature response and population dynamics of soil algae. Algae biomass was taken as 10^7 cells$\cdot$g algae^{-1}, which is not unreasonable considering "cells" refers to colonial fragments as well as single cells. An exponential temperature response was assumed with an optimal temperature of 10° C. Using hourly soil surface temperature measurements (Courtin, unpublished data), hourly acetylene-reduction rates were calculated according to the formula:

$$R = R_o(Q_{10}^{\frac{t-t_o}{10}})P$$

where R_o = rate of acetylene-reduction (umoles$\cdot$m$^{-2}\cdot$hr^{-1}) at temperature t_o($^\circ$ C), R = rate at temperature t, and P = the population of acetylene-reducers when $t > 10^\circ$ C and R = 0. The parameters used were taken from Table 10:

$R_o = (33.4 \times 10^{-6}) \times$ mg algae$\cdot$m^{-2}
$t_o = 0.5^\circ$ C
$Q_{10} = 3.3$

P = 1500 mg on 15 June decreasing to 15 mg on 25 June where it remained for the duration of the season (Table 13). The magnitude of P was derived from 1972 data, but the period of highest values was made to correspond with the most favorable fixation temperatures of 1971 so the estimate represents a maximum potential. The maximum daily reduction rate was 0.35 umoles $C_2H_2\cdot m^{-2}$. The annual increment was estimated to be 14 ug nitrogen m^{-2} ($C_2H_2:N_2$ = 6:1) in the hummocky meadow for 1971. The ratio 6:1 was adopted from Rice (1970).

Using similar parameters for Nostoc commune (Table 10), but

holding P at 20 $mg \cdot m^{-2}$, an estimated 2 ug $nitrogen \cdot m^{-2}$ was contributed by this species to meadow soils.

Nitrogen-fixing bacterial populations have not been specifically studied on Truelove Lowland. A census of aerobic bacteria showed no *Azotobacter*. *Bacillus*, a facultative aerobe capable of nitrogen-fixation, has been isolated from several soils on the Lowland and is relatively abundant in beach ridge soil (Widden *et al.*, 1972). Soils from Alaskan tundra contained no aerobic nitrogen-fixers, but *Clostridium* and *Bacillus* were isolated anaerobically on nitrogen-free medium (Jurgensen and Davey, 1971).

The component of total nitrogen-fixation not attributable to soil algae must be assumed to be by bacteria, probably anaerobic. To estimate the amount of nitrogen fixed by these organisms the parameters from page 22 were used:

$$R_o = 2.25 \text{ umoles} \cdot m^{-2} \cdot hr^{-1}$$

$$t_o = 4.7^\circ \text{ C}$$

$$\text{apparent } Q_{10} = 5.6$$

$$P = 1$$

Using soil temperatures at -7 cm to calculate acetylene-reduction rates, the model gave figures reasonably close to those obtained from assay incubations in the soil pits in 1972 (Fig. 12). Since in the ecosystem most of the nitrogen-fixation occurs in the top 5 cm of the soil profile (Table 1) which is considerably warmer than at -7 cm (Appendix A), the model was driven using soil temperature at -2 cm (Appendix B) to estimate annual nitrogen-fixation. These estimations correspond well with results obtained from assays exposed to light in 1971 (Fig. 13). A factor of 6 was used to convert acetylene-reduction

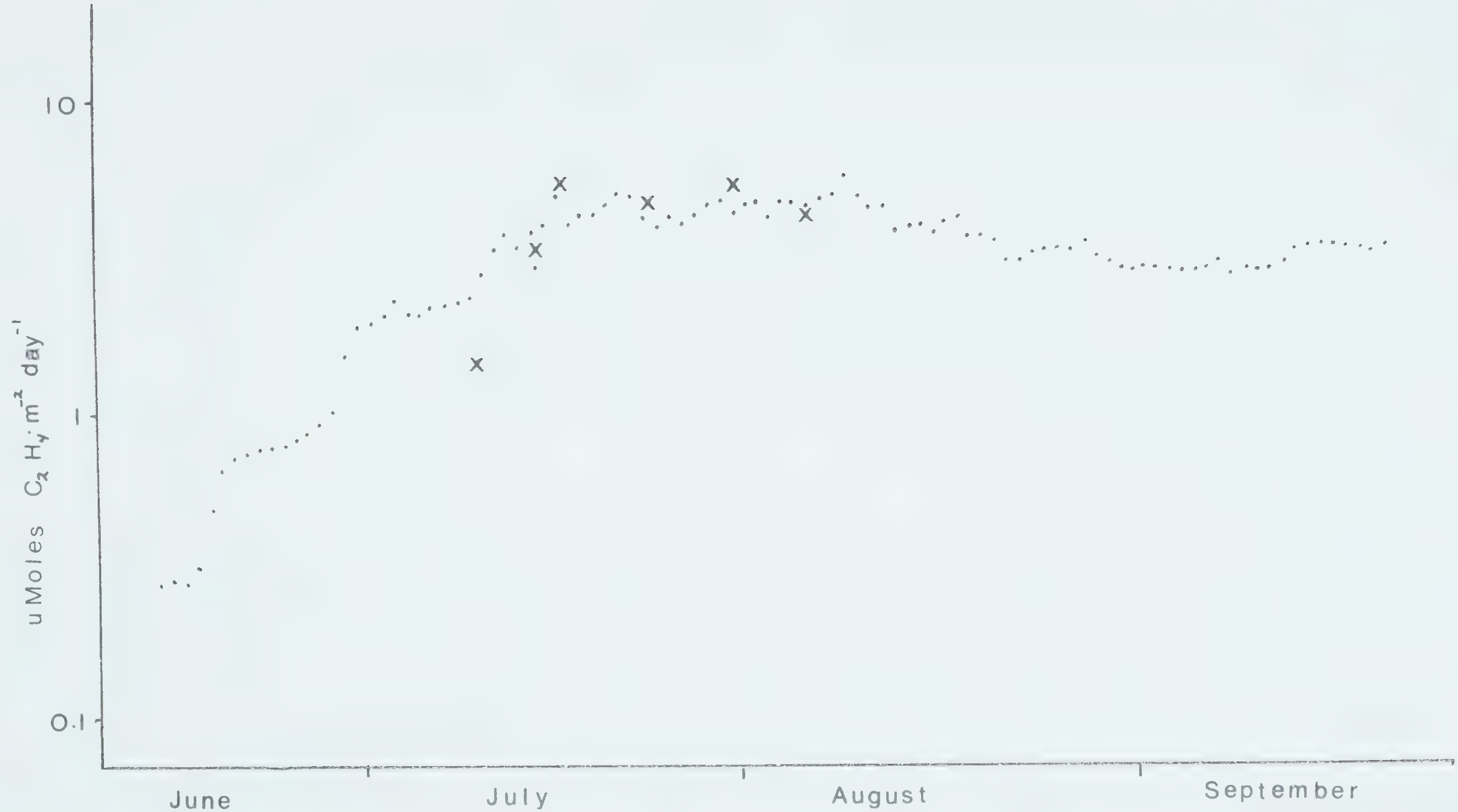


Figure 12. Daily rates of acetylene-reduction in meadow soil on Truelove Lowland as estimated by a temperature-driven model. 1972, -7 cm. Measured values are indicated by X.

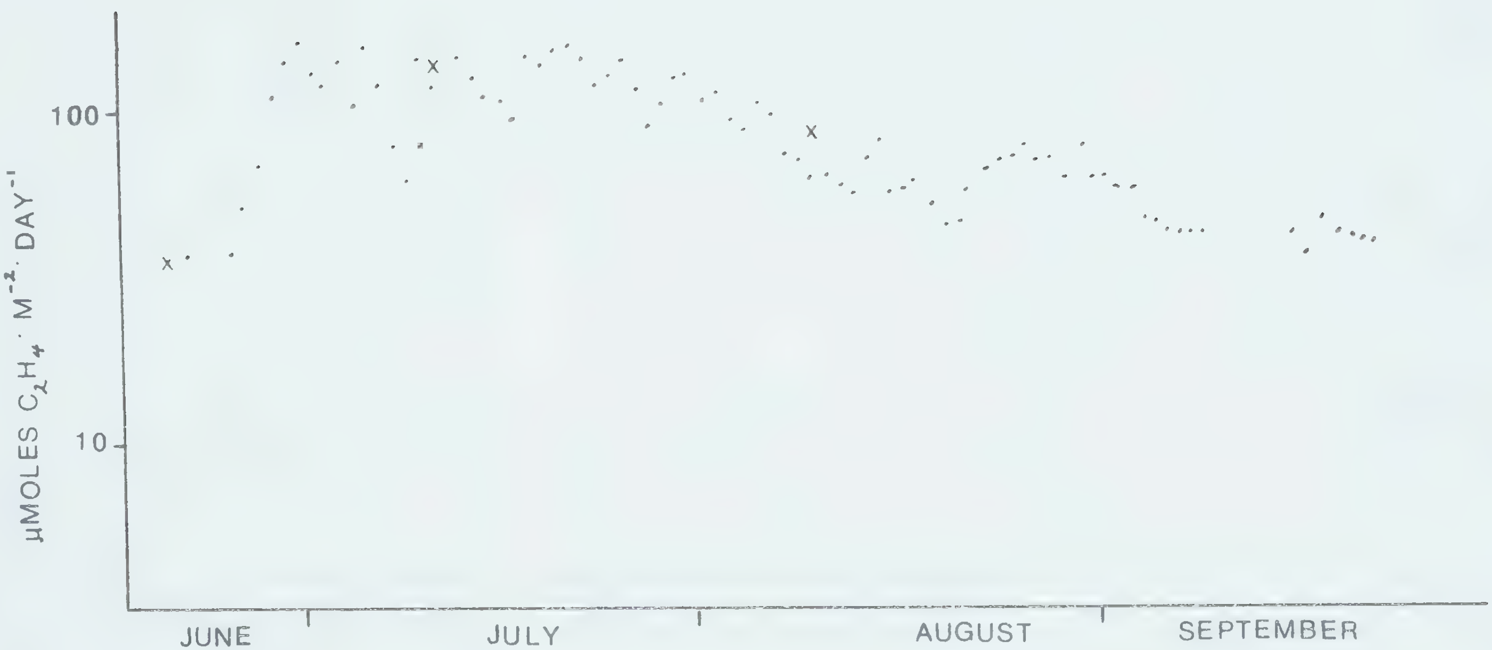


Figure 13. Daily rates of acetylene-reduction in meadow soil on Truelove Lowland as estimated by a temperature-driven model. 1971, -2 cm. Measured values are indicated by X.

to nitrogen-fixation. This ratio was determined by Rice (1970) in a waterlogged system exposed to light. Nitrogen-fixation was thereby estimated to be 190 $mg \cdot m^{-2}$ in 1971 and 65 $mg \cdot m^{-2}$ in 1972.

Parameters for the beach ridge were:

R_o = 0.41 umoles m^{-2} hr^{-1} (Table 2)

$t = 3.6° C$

apparent $Q_{10} = 5.6$

$P = 1$

The model is not as accurate in estimating beach ridge nitrogen-fixation (Fig. 14), probably because of the low water potentials which develop in these soils. Sufficient data are not available to incorporate this factor into the model. Nevertheless, the model is useful in a relative sense, and data from 1971 assays differ little from the calculated estimates (Fig. 15). The ratio between acetylene-reduction and nitrogen-fixation in beach ridge soil probably approaches 3:1 inasmuch as this system is so much more aerated (Rice, 1970). In beach ridge soils there was an estimated nitrogen input of 30 $mg \cdot m^{-2}$ in 1971 and 7 $mg \cdot m^{-2}$ in 1972.

Asymbiotic nitrogen-fixation on Truelove Lowland is therefore primarily a function of bacteria rather than algae (Table 14). This is in contrast to nitrogen-fixation in other tundra sites (Alexander and Schell, 1972) and peat lands (Granhall and Selander, 1972) in which blue-green algae are much more important. Nitrogen-fixation by lichens is not as important as was once supposed (Russell, 1940). Symbiotic nitrogen-fixation is not important on the Lowland. This may be a unique feature of the High Arctic since legumes have been collected from the western Canadian Archepelago, Greenland, and northern Baffin

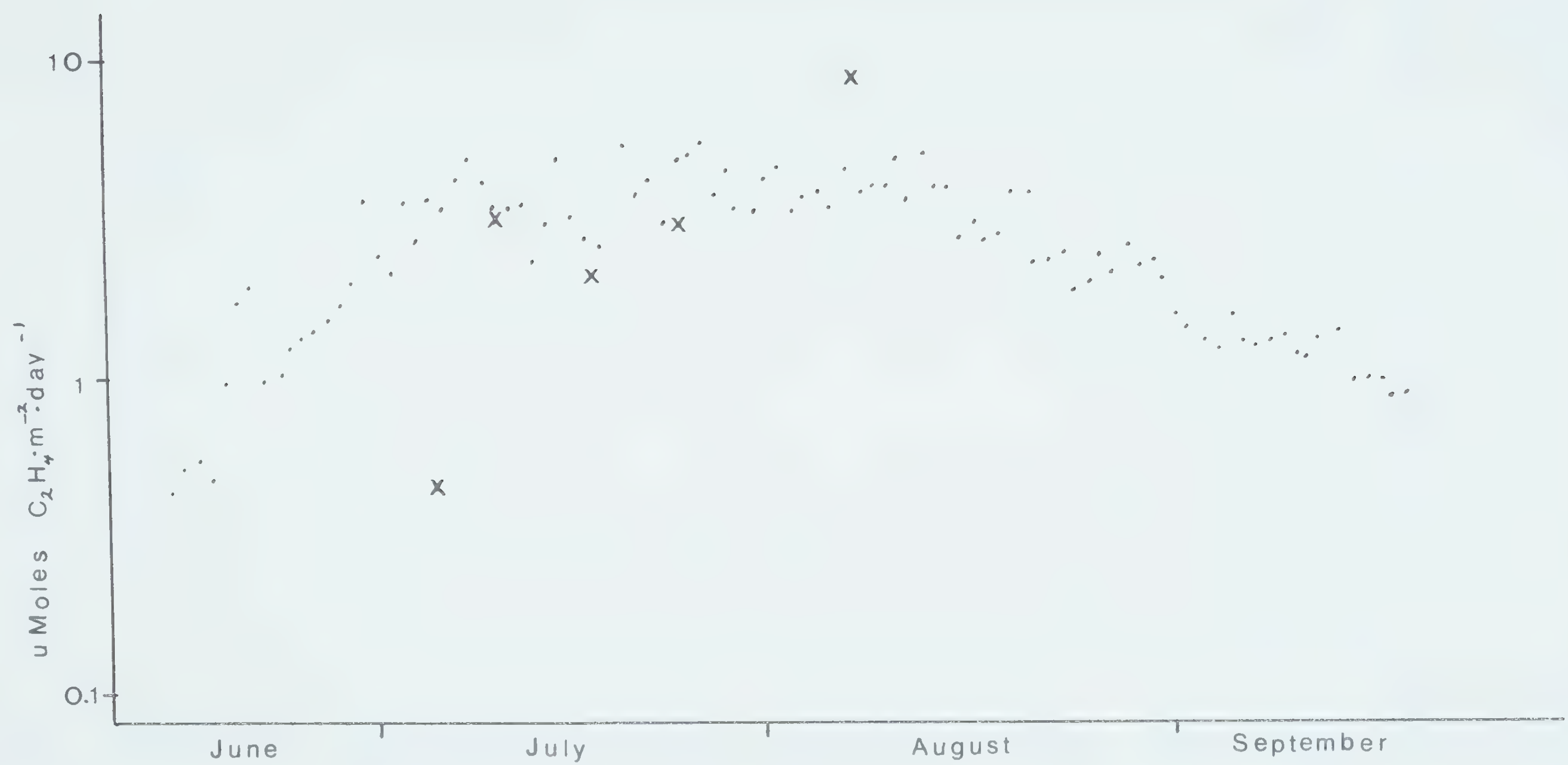


Figure 14. Daily rates of acetylene-reduction in beach ridge soil on Truelove Lowland as estimated by a temperature-driven model. 1972, -7 cm. Measured values are indicated by X.

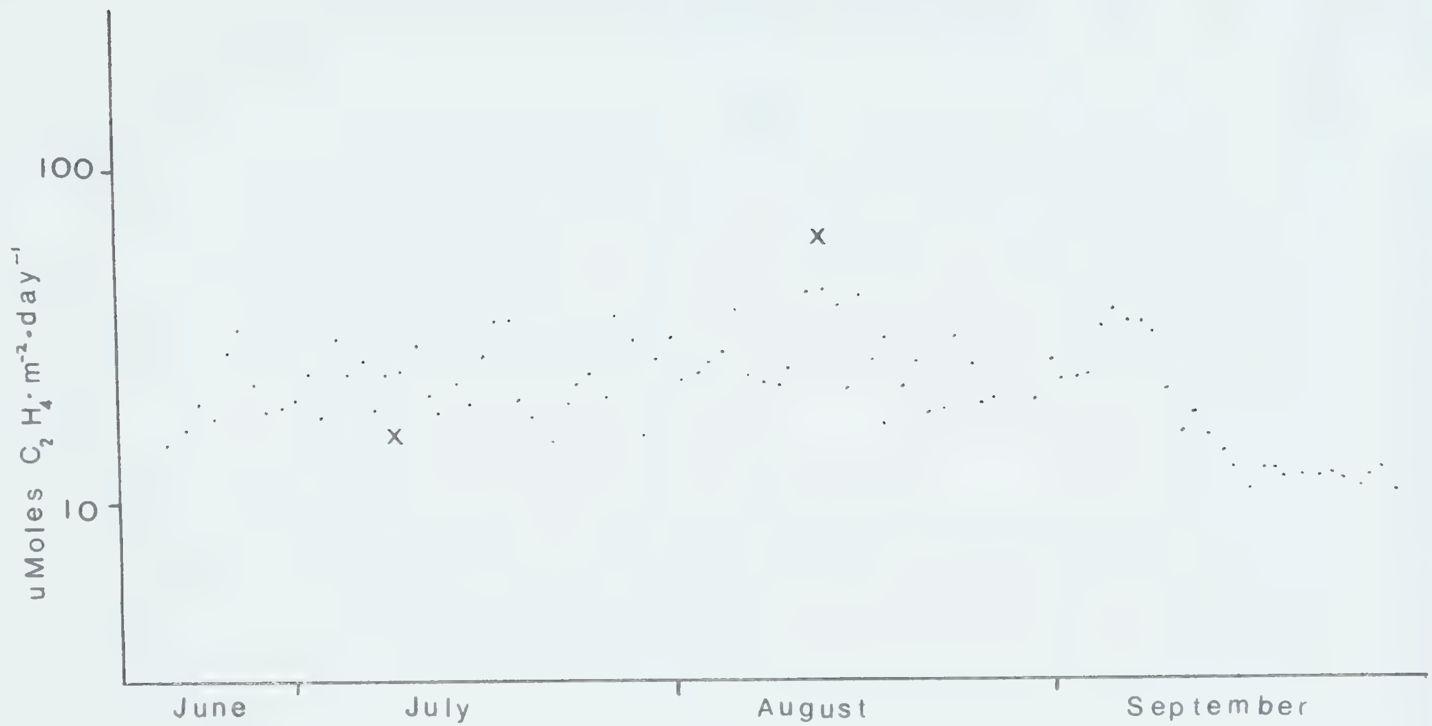


Figure 15. Daily rates of acetylene-reduction in beach ridge soil on Truelove Lowland as estimated by a temperature-driven model. 1971, -2 cm. Measured values are indicated by X.

Table 14. Maximum acetylene-reduction rates and annual nitrogen-fixation rates on Truelove Lowland.

Habitat	Maximum acetylene-reduction rate ($umoles \cdot m^{-2} \cdot hr^{-1}$)	Annual N Fixation ($mg \cdot m^{-2} \cdot yr^{-1}$)
Beach ridges	3.18	30
Frost boil meadows	7.53	-
Hummocky meadows	5.18	190
Wet meadows	1.87	-
Soil algae (meadows)	0.35	14×10^{-3}
Nostoc commune	(53 uumoles•mg•hr)	2×10^{-3}
Peltigera aphthosa	(5.1 uumoles•mg•hr)	-

Island (Porslid, 1964), and Alnus sp. which is known to fix nitrogen (Zavitkovski and Newton, 1967) is found in low arctic sites (Johnson, 1967).

Taken as a whole, Truelove Lowland is a remarkably closed ecosystem. The nitrogen flux by bird migrations is insignificant inasmuch as the avian population on the Lowland is so depauperate (Pattie, 1972). Muskoxen are residents of the Lowland, and predators are even less abundant than birds, so mammalian transport of nitrogen is virtually nil.

Nitrogen was not detected in snow or summer precipitation. The relatively short period of time the sea is ice-free (two to three weeks) minimizes nitrate import from salt spray. By far the greatest avenue of nitrogen exchange with other systems is biological nitrogen-fixation.

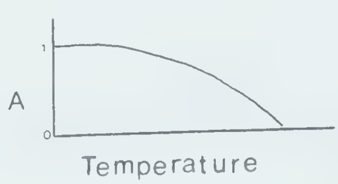
However, the terrestrial ecosystems of the Lowland are very much open systems with regard to the aquatic system. Lake surfaces account for over 20% of the Lowland area (Bliss, 1972). Into this system is carried 27% of the plant litter (Muc, unpublished data). Lake sediments, presumably wind blown, can be found on many meadows. Invertebrates exploit both systems with little regard for shoreline boundaries. Nitrogen-fixing algae (Nostoc pruniforme) form impressive blooms in several of the lakes. Until data on the nitrogen regime of Lowland lakes are available, little can be said concerning the nitrogen budget of the entire Lowland ecosystems.

SUMMARIZING MODELS

A model based on the exaggerated response of nitrogen-fixation to temperature was developed as a tool to estimate seasonal fixation rates, but was not intended to be mechanistic. Actually there is a host of interacting variables influencing the spacial and temporal distribution of nitrogen-fixing organisms and the rate of nitrogen-fixation. Figure 16 suggests some of the more distinct factors affecting biological nitrogen-fixation.

The oxygen regime of soil presents one of the more intriguing problems, for while nitrogen-fixation is an anaerobic process, the nitrogen-fixing organisms depend on high energy substrates associated with aerobic metabolism (pg. 23 _et seq_.). The gross interface between aerobic and anaerobic soil varies over a season with the water table. But perhaps a more functional interface is that which is found within a soil particle. Greenwood and Goodman (1967) demonstrated, both theoretically and experimentally, that the center of soil aggregates, even in well-aerated soils, may be anaerobic, oxygen being consumed as it diffuses into the soil particle.

Assume a soil particle to be a homogeneous sphere with volume $\frac{4}{3}\pi$ into which O_2 diffuses to a depth of $\underline{A}$ so that $\frac{4}{3}\pi\,(1-A)^3$ represents the volume of anaerobic phase of the particle and $\frac{4}{3}\pi\,(1-(1-A)^3)$ is the volume of the aerobic phase. $\underline{A}$ varies between 1 and 0 with temperature as a reciprocal function of aerobic metabolism.



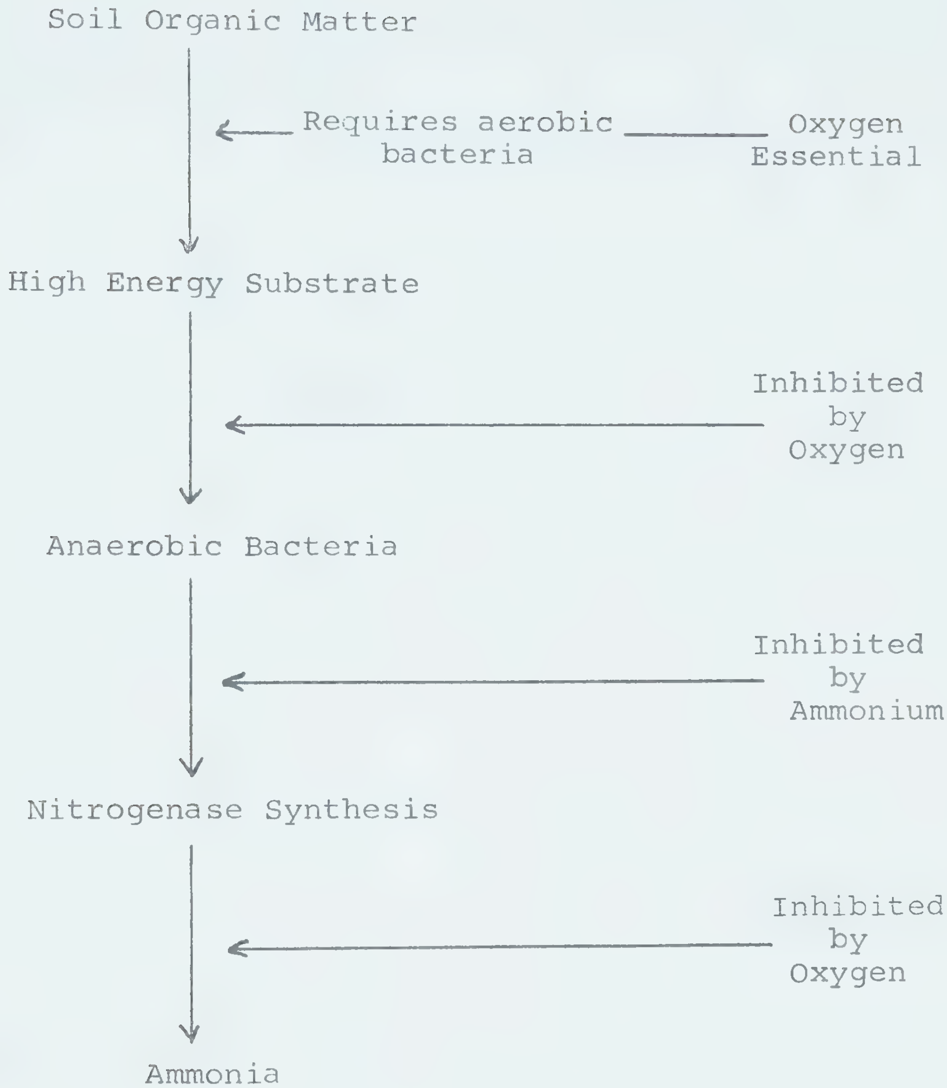
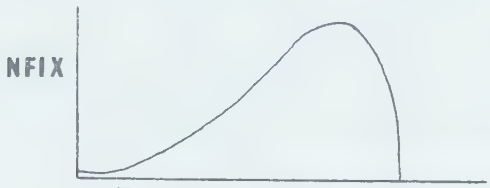


Figure 16. Flow diagram for anaerobic nitrogen fixation.

The rate of anaerobic nitrogen-fixation (NFIX) is a function of both aerobic and anaerobic volumes, the relative magnitude of each varying with temperature:

$$NFIX = (4/3\pi)^2 \cdot (1 - (1 - A)^3) \cdot (1 - A)^3$$



The shape of this curve is reminiscent of the temperature response of acetylene-reduction, i.e., a steep exponential foreslope and a rapid decrease at temperatures far below lethal temperatures of the nitrogen fixers. Indeed, when A is zero because of high microbial activity NFIX is 0.

Implicit in this argument is that NFIX is a function of aerobic volume rather than activity. Since the function of aerobiosis is to provide digested but unutilized substrate, this implication may be valid.

The rate of nitrogen-fixation (190 mg.m^{-2}.yr^{-1}) appears to be comparable to more temperate regions (cf. Hardy et al., 1973), but when the rate is related to the organisms responsible for the transformation on Truelove Lowland, it becomes excessive. Bacterial biomass is ca. 9% nitrogen. Therefore, 190 mg nitrogen would represent 2 g bacterial production.m^{-2}. If the nitrogen-fixing anaerobic population (B) is heterotrophic, and can effectively compete for organic nitrogen, a static population ($\frac{\Delta B}{\Delta t} = 0$) would fix little nitrogen. Nitrogen would be sufficiently available in senescent cells. Nitrogen-fixation would be appreciable only when $\frac{\Delta B}{\Delta t} > 0$. If the Lowland nitrogen-fixers are 100% efficient as heterotrophs, there was a net production of 2 g anaerobic

biomass$\cdot m^{-2}$ in 1971, ca. 10 x the standing crop of aerobic bacteria (Widden, et al., 1972). If, however, the nitrogen-fixers can compete for organic nitrogen only ineffectively, nitrogen-fixation rates represent an estimate of gross production and $\frac{\Delta B}{\Delta t}$ may approach 0.

The relationship of nitrogen-fixation to bacterial production lies between these two extremes (net and gross production). The dependence of nitrogen-fixers for high energy substrates, and their apparent insensitivity to normal amounts of NH_4^+ in the soil suggest that the relation between nitrogen-fixation and anaerobic productivity is nearer the latter case. Atmospheric nitrogen may well be the primary source of nitrogen for these populations.

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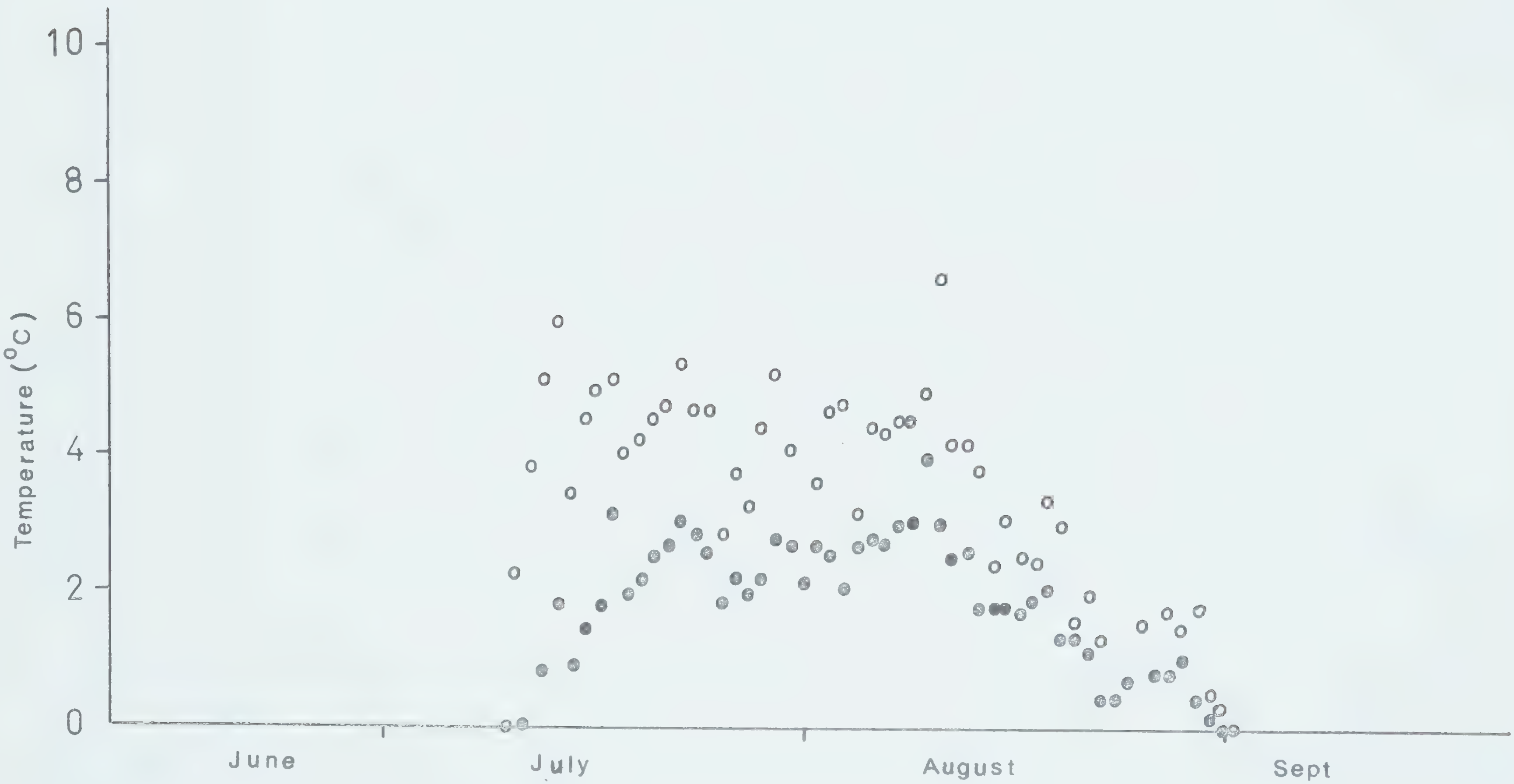
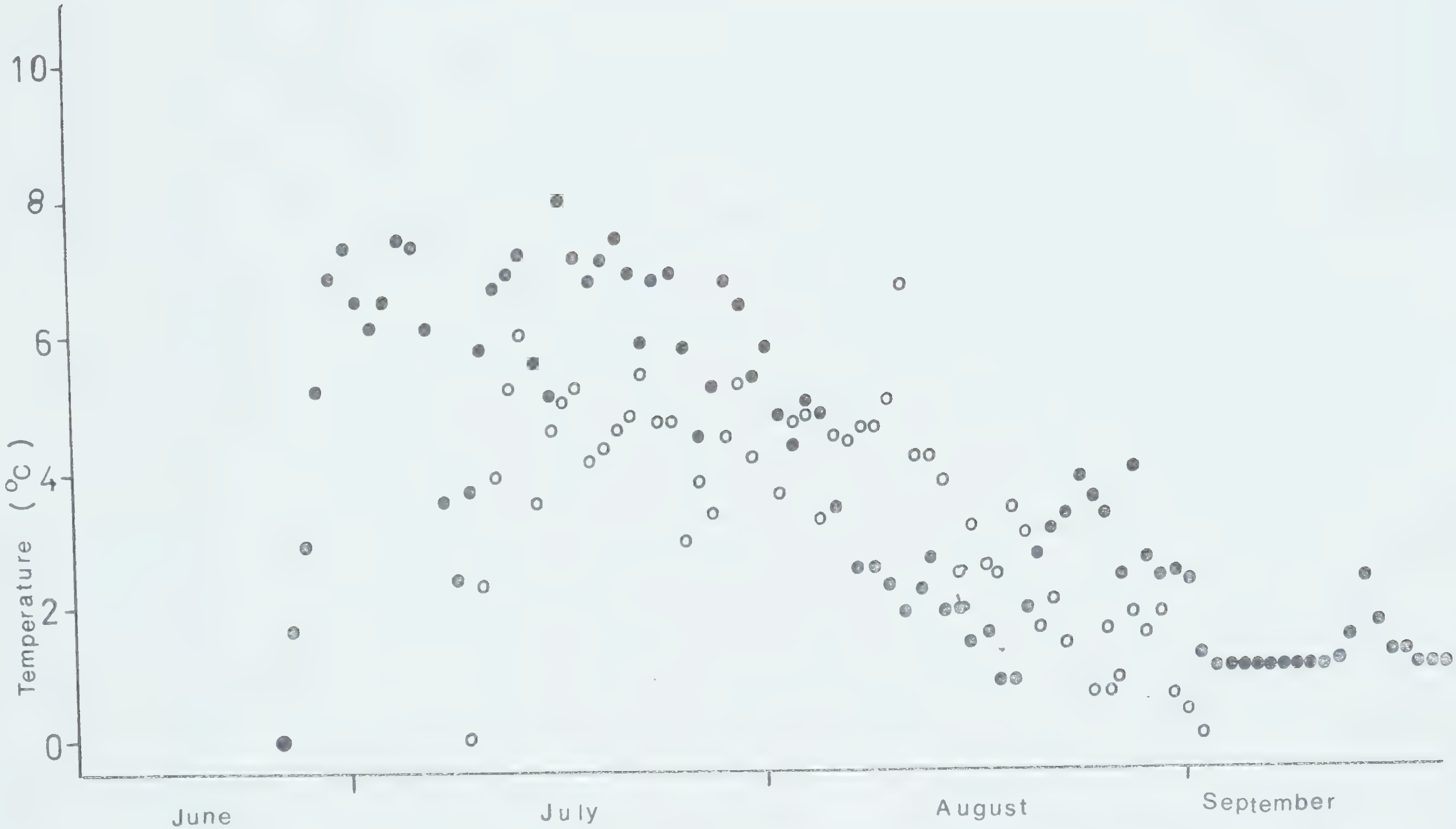
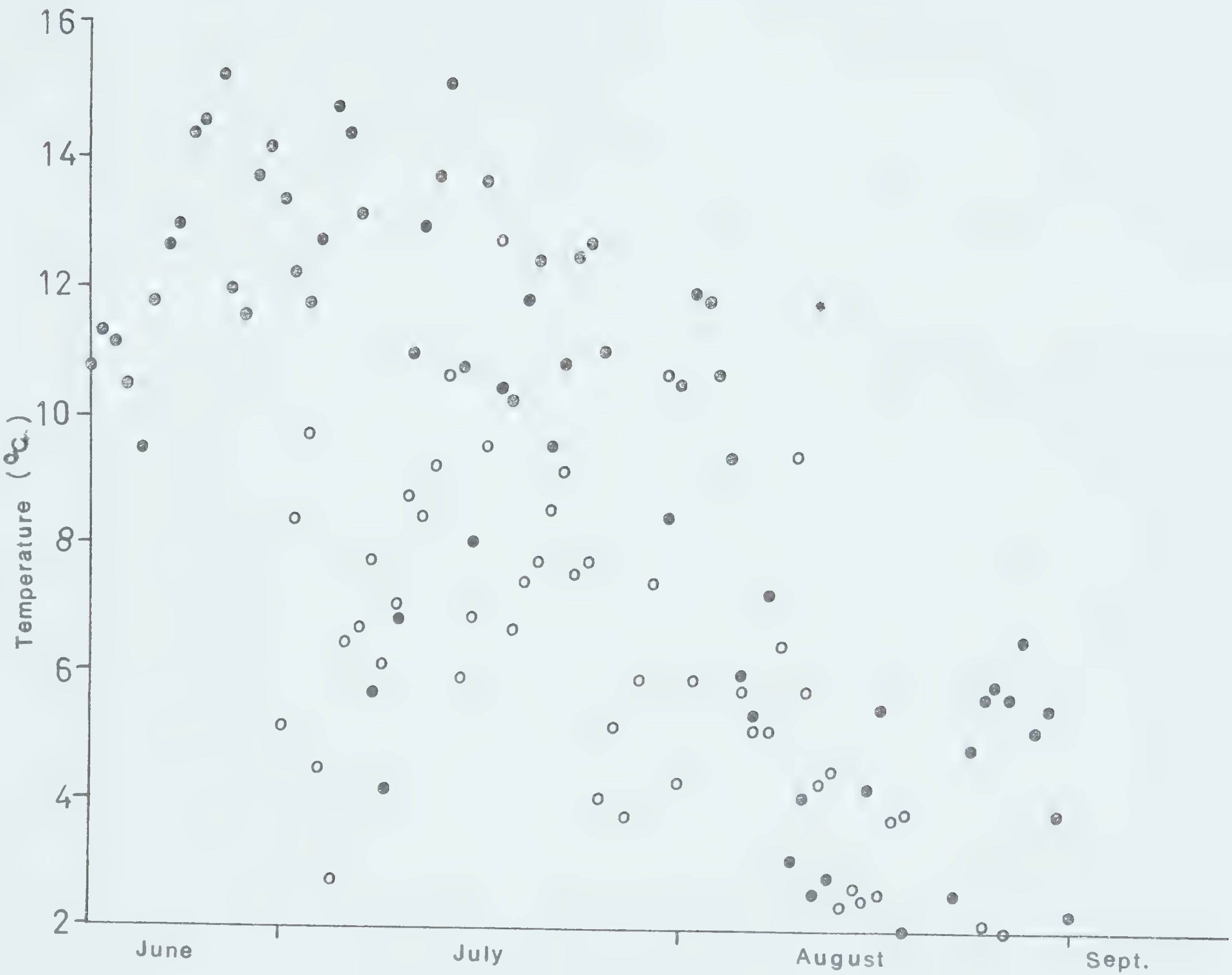


Appendix A. Daily mean soil temperature in meadow soils on Truelove Lowland 1972.
o = -2 cm; ● = -7 cm.



Appendix B. Daily mean soil temperature in meadow soils on Truelove Lowland (-2 cm).
● = 1971; o = 1972.



Appendix C. Daily mean soil temperature in beach ridge soils on Truelove Lowland. ● = 1971; o = 1972 (-2 cm).